Spatial and temporal variation in growth and age composition of the temperate wrasse Notolabrus fucicola in Tasmanian waters

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Declarations

I hereby declare that this thesis is my own work, except where due acknowledgement is given, and that the material presented here has not been submitted at another university for the award of another degree or diploma.

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Graeme Paul Ewing

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Abstract

The mechanisms that determine the age and size structure of a population are not well understood for temperate reef species and are functionally divided into pre-settlement and post-settlement processes. Their relative importance in structuring populations can be inferred from spatial comparisons of adult age composition and growth rates, provided factors that obscure or bias the ability to detect signals from early life history are considered. These factors include migration, fishing mortality and methodological issues such as ageing errors and size-selectivity of sampling gears.

The biological features that promote *Notolabrus fucicola* as a suitable species for demographic research and the highly variable hydrology of the east and southeast coasts of Tasmania, provide an opportunity for examination of the relative roles of pre-and post-recruitment processes in structuring temperate reef populations. In addition, *N. fucicola* is the primary target of a commercial live wrasse fishery that has developed over the last decade in Tasmania, necessitating an understanding of its population dynamics for effective management.

Notolabrus fucicola were collected using baited traps from six locations around the east and southeast coasts of Tasmania. A methodology for age estimation was developed using thinly sliced transverse sagittal otolith sections and the periodicity and timing of increment formation, location of the first annual increment and precision of age estimations were validated.

A size-selectivity function for the traps was calculated directly from sampling an isolated population of *N. fucicola* of known size structure, generated from a simulated fish-down using tags. The selectivity function was used to reconstruct the raw size and age structures from which fishing mortality was estimated. Fishing mortality varied spatially, with strong mortality prior to the minimum legal size limit implied at some sites.

Spatial comparisons of growth were not biased by fishing mortality and indicated that growth rates followed the sea surface temperature gradient, but did not follow trends in fishing mortality, diet or reef structure. Given that growth is sensitive to resource-limitation, the spatial trend in growth rates suggested that populations of *N. fucicola* were not structured by post-settlement density-dependent mortality.

Spatial and temporal comparisons of selectivity-corrected age compositions, whilst primarily detecting differences in the level of fishing mortality between sites, indicated low variation in relative year class strength. This result is consistent with recent findings suggesting that *N. fucicola* are well adapted to maximize larval survival despite the highly variable coastal hydrography. Thus, it is likely that populations of the temperate wrasse *N. fucicola* are primarily structured by larval supply.

Chapter 1: General Introduction

Identifying the processes that determine the age and size structure of a population is a fundamental goal of ecological research (Hughes, 1990). These processes are functionally divided into pre-settlement processes (governing egg and larval survival to settlement) (Doherty and Fowler, 1994, Doherty, 1992, Pitcher, 1992) and post-settlement processes (governing growth and survival after settlement) (Forrester, 1995, Steele and Forrester, 2002, Steele, 1997, Tupper and Boutilier, 1995). The relative importance of pre- and post-settlement processes in structuring reef fish populations in open marine systems is still poorly understood and may also vary in time and space (Jones, 1984a, Caselle, 1999). Post-settlement factors shown to influence population structure include food availability (Bradford, 1992), reduced growth (Gust *et al.*, 2002, Tupper and Boutilier, 1995), shortage of suitable habitat (Tupper and Boutilier, 1995 , Nitschke *et al.*, 2002, Jones, 1984a), predation (Steele, 1997) and fishing mortality (Choat *et al.*, 2003). However, population structure is more likely to be influenced by density-dependent processes in juveniles than adults (Rickman *et al.*, 2000), due to generally decreasing predation with increasing size (Gust *et al.*, 2002).

Typically research into early life history phases involves capture of fish as they arrive at reefs or briefly after settlement (Doherty, 1987, Steele, 1997), or experimental manipulations of the densities of predators (Steele and Forrester, 2002), settlers (Tupper and Boutilier, 1995) and/or conspecifics (Tupper and Boutilier, 1995, Jones, 1984b). Such methods are expensive. They require considerable logistic support and repeated sampling programs over several years to adequately measure inter-annual variation in settlement abundance (Meekan *et al.*, 2001).

Adult age structure, particularly from long-lived species, can also provide a means of reconstructing a history of settlement events (Meekan *et al.*, 2001). However, post-settlement density-dependent mortality may obscure signals from settlement. In addition, variation in density-dependent processes govern the extent to which strong peaks in settlement are evident in the size and age structures of adult populations (Jones, 1984b). Growth is strongly influenced by density-dependence through mechanisms such as resource-limitation and competition for shelter, resulting in less time spent foraging (Tupper and Boutilier, 1995). Evidence of density-dependence may be detectable by comparing overall growth patterns among reefs where there are varying ratios of population density to food resources (Barrett, 1999) or juvenile habitat (Jones, 1984b). This method of detecting density-dependent conditions is particularly effective for site-attached species, where evidence of density-dependent growth is preserved for longer in the absence of migration and emigration. Furthermore, spatial and temporal comparisons of age composition and growth are particularly informative because the factors that influence early life history events vary in time and space.

Notolabrus fucicola is a reef associated labrid that is distributed throughout temperate waters of south eastern Australia and New Zealand (Edgar, 1997, Gommon *et al.*, 1994, Russell, 1988, Denny and Schiel, 2001). They are one of the dominant predators on inshore exposed rocky reefs, feeding on benthic invertebrates, particularly crustaceans and molluscs (Jones, 1988, Denny and Schiel, 2001). In Tasmanian waters they are long lived (17 years), site-attached, experience low adult mortality rates (Barrett, 1995a) and are commercially exploited for live export (Lyle and Hodgson, 2001). *Notolabrus fucicola* are gonochoristic and have an extended

spawning season from August to January (Barrett, 1995a). Their eggs hatch after 2-5 days and competent larvae settle on inshore reefs after 30 to 70 days at approximately 12 mm in length (Welsford, 2003a).

Notolabrus fucicola are well suited for examining age composition and spatial growth variability because their longevity provides numerous year classes for comparison. Their dispersive larval phase (Welsford, 2003a), in concert with complex and variable local hydrology (Harris *et al.*, 1987), is likely to result in a well-mixed genetic stock over the spatial scale of the area studied (Welsford, 2003a). Furthermore, Ward (2001) found limited genetic differentiation in fish sampled in the south eastern region of Australia due to influential currents and a lack of major oceanographic and environmental barriers to gene flow. This allows spatial differences to be attributed to differences inherent in the sites sampled, rather than genetic differences among populations. Furthermore, low adult mortality and site-attachment reduce the dilution of recruitment signals caused by migration and emigration. These life history traits indicate that *N. fucicola* are a suitable species for inferring the relative importance of pre- and post-settlement processes in structuring adult population structure through determination of age composition and spatial comparisons of age structure and growth.

Populations of other temperate wrasses have been found to be structured by post-settlement processes in early life through conspecific density-dependent growth suppression (Tupper and Boutilier, 1995, Jones, 1984b, Levin *et al.*, 1997). Barrett (1999) concluded that populations of *N. fucicola* were not resource-limited because growth rates were similar among sites with similar habitats. However, these conclusions were based on small sample sizes, the ageing methodology was not

robustly validated, and environmental factors likely to influence growth (such as temperature, diet or reef characteristics) were not examined among sites to ensure similarity.

The Tasmanian live wrasse fishery targets *Notolabrus tetricus* and *N. fucicola*, however catches are focused on the east and southeast coasts where landings are predominantly *N. fucicola* (Lyle and Hodgson, 2001). Assessment of spatial variation in growth rates over the geographic range of the *N. fucicola* fishery would allow assessment of the appropriateness of the current Statewide scale of management. An additional advantage of age and growth research with a spatial component is to provide fishery independent estimates of fishing mortality, because the catch and effort data supplied by the wrasse fishery is of varying quality and, due to the spatial scale of reporting, may mask localised depletions. Strong fishing mortality has the potential to bias population parameters such as adult age structure and growth (Ferreira and Russ, 1995), and therefore mask signals from settlement events for much of the population. Thus, fishing mortality must be considered when examining growth variation and reconstructing age composition to examine the factors likely to drive variations in year class strength.

Estimating the growth and age structure of fish has become routine in fisheries research due to recent advances in fish ageing methodology (Campana, 2001). Procedures such as otolith sectioning (Beamish, 1979), bomb radiocarbon dating (Kalish, 1993), otolith microchemistry (Kalish, 1989, Campana, 1999) and back-calculation (Campana, 1990) have become powerful tools for fisheries research. However, validation of age estimates is essential to these methods, but is often not comprehensively assessed (Campana, 2001, Beamish and McFarlane, 1983).

Campana (2001) stressed that validation is more than determining the periodicity of increments and identified the essential requirements for validation of ageing methodologies. In addition to poorly validated age research, confusing use of ageing terminology has also led to inaccurate age estimates which can dramatically affect the outcomes of fisheries modelling (Clark, 1999, Bradford, 1991).

Other biases may relate to fishing gear used to sample a population which rarely targets all components of the population equally (Ricker, 1975). Biases likely to be caused to estimates of size and age structure by gear selectivity have not always been considered and have rarely been quantified in age and growth research (Finstad *et al.*, 2000). A selectivity function can be generated for fishing gear and can be used to adjust the size and age structure of a sample to reflect that of the sampled population (Finstad *et al.*, 2000). Direct methods of generating a selectivity function (utilising a population of known size structure), are considered more robust than indirect methods (Jensen and Hesthagen, 1996). However, direct methods require very large sample sizes in open marine systems to adequately represent the sampled population (Millar, 2000, Anganuzzi *et al.*, 1994). The life history of *N. fucicola* (ie. site attached to consolidated reef habitat) (Barrett, 1995b), offers the potential to directly measure the selectivity of sampling gear using a considerably smaller population resident on an isolated reef.

The aims of this research were to generate selectivity-corrected estimates of size and validated age structure for *N. fucicola* populations and to examine growth and year class strength over a large spatial scale. Such information could contribute to the understanding of processes that structure populations of temperate reef fishes and provide information on population parameters essential to improve management of

the live fishery for *N. fucicola.* To achieve these complementary aims, *N. fucicola* were sampled from six individual rocky reefs on the east and southeast coasts of Tasmania to determine size and age structure. The interpretation of increments in transversely sectioned sagittal otoliths was comprehensively validated and age structure and growth rates estimated for each site. A selectivity function for the sampling gear was derived and the size and age structure of *N. fucicola* at all sites were corrected for size-selectivity biases. Fishing mortality was estimated for each site from selectivity-corrected size structure and catch curve analysis. Spatial trends in growth rates were examined to infer the likely role of density-dependence in structuring *N. fucicola* populations. Selectivity-corrected age compositions were examined, with consideration of fishing mortality, to determine the relative year class strengths of individual populations of *N. fucicola.* Such information was then used to infer the likely significance of pre- and post-settlement processes in structuring the populations of this temperate reef fish.

The specific aims of each component of the thesis is outlined below:

Chapter 2: Validation of age and growth estimates using thin otolith sections from the purple wrasse *Notolabrus fucicola*

To generate estimates of age and growth of *N. fucicola,* with particular attention to the validation of the accuracy and precision of annulus interpretation from thinly sliced otolith sections.

Chapter 3: Spatial variation in the growth of *Notolabrus fucicola*

To produce robust estimates of growth over large spatial scales involving biologically sensible parameters and to infer the possible role of post-settlement density-dependence in structuring populations of *N. fucicola.*

Chapter 4: Size-related biases in trap caught samples of *Notolabrus fucicola* trap caught from populations exposed to fishing mortality

To generate a selectivity function for the sampling gear and estimate selectivity-corrected size structure and instantaneous mortality estimates all sampling sites. The extent of spatial variation in fishing mortality is also examined using catch curves generated from selectivity-corrected age structure.

Chapter 5: Spatial and temporal variation in the age composition of *Notolabrus fucicola*

To determine the selectivity-corrected age structure of discrete populations of *N. fucicola*, examine temporal and spatial patterns in relative year class strengths over large spatial scales and infer the likely significance of fishing mortality and settler densities in determining population structure.

Chapter 6: General discussion

Spatial and temporal trends in relative year class strengths and spatial trends in the growth rates are discussed with reference to the population structure of *N. fucicola* and the management of the Tasmanian wrasse fishery.

Chapter 2: Validation of age and growth estimates of the purple wrasse *Notolabrus fucicola*

2.1 Introduction

The interpretation of periodic increment structure in fish bony parts is a fundamental tool in estimating age structure, growth rate and mortality of fish populations. Otoliths are often used for this purpose because they incorporate periodic and incremental structure on a daily, seasonal and/or annual basis. The most common approaches used to examine otolith increment structure involve examination of whole otoliths (usually immersed in a liquid medium) (Hyndes *et al.*, 1992), "broken and burnt" otoliths (where the otolith is broken transversely through the primordium and heated to accentuate the increment structure) (Francis *et al.*, 1992), and examination of thin sections sliced through the primordial region (Beamish, 1979). Thin transverse otolith sections improve the detection of increment structure (Collins *et al.*, 1989). This is particularly the case in otoliths from older fish due to a change in the deposition of zones from the ventral surface to the proximal surface where they are harder to detect from unsectioned otoliths, which can lead to underestimation of age (Hyndes *et al.*, 1992, Collins *et al.*, 1989, Campana, 1984, Beamish, 1979, Ferreira and Russ, 1994, Treasurer, 1994).

Within age and growth research, there has been a history of inadequate attention to validation (Beamish and McFarlane, 1983), with recent attention given to the neglected distinction between validation of the periodicity of increment formation and that of the accuracy of age estimates (Campana, 2001). The most commonly used method of validating the periodicity of increment formation is marginal increment analysis (MIA) which utilises temporal trends in the formation of increments on the

growing edge of the otolith. Campana (2001) criticised MIA because of the subjectivity of interpretation of the otolith growing edge and because unlike methods that measure absolute age (such as known-age marked release studies and bomb radiocarbon analyses), MIA does not allow the accuracy of age estimates to be calculated. He conceded that MIA can be applied validly provided that samples are randomised before examination, a minimum of 2 cycles are examined, cycles are determined using a statistical test, validations are considered age-specific and the timing of formation of the first increment is determined.

The age and growth of *N. fucicola* in Tasmanian waters has been estimated previously using counts of opaque zones from whole otoliths and tag recapture methods, although sample sizes were small (58 and 82, respectively) (Barrett, 1995a). In addition, otolith increment periodicity was not validated, timing of the formation of annuli and the precision of age estimates were not examined and criteria for interpretation of the otolith margin were not defined.

The aims of this study were to generate age estimates for *N. fucicola* using counts of opaque growth zones in thin transverse otolith sections and to address issues of the validation of their accuracy and precision.

2.2 Materials and methods

2.2.1 Sampling

A total of 2826 purple wrasse (*Notolabrus fucicola*) were sampled from the east and southeast coasts of Tasmania between July 1999 and January 2001. Samples were collected monthly until January 2000 after which sampling was conducted on a 3 monthly basis. Larger fish (>130 mm FL) were caught using baited fish traps set on

coastal rocky reefs in less than 5 metres of water. Smaller fish (<130 mm FL) were not vulnerable to the fish traps, so newly settled 0+ fish were caught from artificial habitats deployed inshore and at similar depths to the traps (Welsford, 2003a). One plus fish were also collected with rotenone from a sub-tidal rock-pool adjacent to the Point Bailey site.

2.2.2 Laboratory procedures

Each fish was sexed and fork length (to the nearest mm) and total weight (to the nearest g) recorded. Gonads were removed and weighed (to the nearest 0.1 g) from mature fish. A gonado-somatic index (GSI) was calculated ($GSI = 100 \times Wt_g / Wt_s$, where Wt_g is the gonad weight and Wt_s is the somatic fish weight). The timing of peak spawning was inferred from that point when annual peak GSI values commenced their decline. This time of peak spawning was established as the birthdate for age estimations. Sagittal otoliths (hereafter "otoliths") were removed, cleaned, dried, and if intact, weighed (to the nearest mg).

2.2.3 Terminology

The terminology used in this paper is consistent with Kalish *et al.* (1995). The term "translucent zone" refers to a zone that appears brighter under transmitted light relative to an adjacent "opaque zone" which appears darker under transmitted light. The term "annulus" refers to a validated growth zone, contiguous across the proximal region (ventral to the sulcus acusticus) of the otolith section and which has an annual periodicity. "Annuli" are the structures enumerated to estimate age (Fig. 2.1). The term "otolith growing edge" refers to the outer edge of the otolith section at the proximal surface, ventral to the sulcus acusticus. The term "marginal increment" refers to the translucent region beyond the last identifiable opaque zone and adjacent

to the otolith growing edge. The term otolith "core" refers to the uniformly opaque zone inner and concentric to the first clear translucent zone and concentric to the "primordium" which refers to the small area of initial otolith growth.

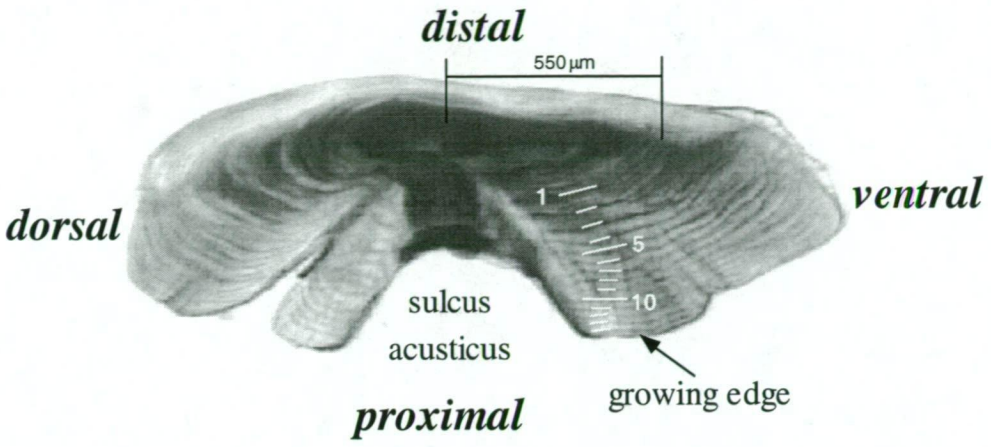

Figure 2.1: Photomicrograph (transmitted light) of a transverse otolith section from *Notolabrus fucicola*. The scale bar indicates the distance from the primordium to the first annulus (determined from examination of the otoliths of young-of-the-year). Opaque zones are marked and age was estimated at 14.9 years (sample was collected 24th August and the assigned birthdate was 1st of October), with a wide marginal increment.

2.2.4 Otolith preparation and interpretation

One otolith from each adult was mounted in a block of polyester casting resin and sectioned transversely through the primordium, to a thickness of 250 to 300 µm, with a lapidary diamond saw. Sections were mounted on a glass slide with polyester resin. Each mounted section was examined with a stereo-microscope at 25X magnification using transmitted light to count opaque growth zones and to categorize the otolith proximal growing edge (ventral to the sulcus acusticus) as having a wide, intermediate or narrow translucent margin (relative to the width of the next inner translucent zone). Mounted sections were also viewed with a compound microscope

at higher magnification (100X) using transmitted light for more detailed examination of the otolith growing edge.

Otoliths were rejected if the increment structure was optically unclear or confusing, or if the primordium could not be identified. Otoliths were read with no reference to fish length, weight or date sampled.

2.2.5 Precision of age estimates

The primary reader (Reader A) examined all otoliths (n = 2826) and then re-read the first 1011. A secondary reader experienced in examination of transverse sagittal otolith sections (Reader B), read a random sub-sample of 342 otoliths. The precision of age estimates between and within readers was calculated using the index of average percent error (APE) (Beamish and Fournier, 1981) and examined visually using age bias plots (Campana, 2001). The age frequency distributions generated by the second and third readings were tested for age bias against the age frequency distribution generated by the initial reading, using a G-test for goodness of fit (Sokal and Rohlf, 1995).

2.2.6 Validation of first annual increment

To confirm the position of the first annual increment, the transverse radii of whole sagittae from 0+ and 1+ fish were measured, using image analysis software, and plotted against month sampled. These radii were then compared with the radii of the inner opaque growth zones in the transverse plane of sectioned otoliths from older fish, measured using image analysis software.

2.2.7 Validation of the periodicity and timing of opaque zone formation

The periodicity of opaque zone formation was determined by analysing the temporal pattern of the marginal increment, using 100X magnification. Indices of completion (C) were calculated for a sub-sample of 1575 transverse sectioned otoliths, using the formula:

$$C = 100 \times W_n / W_{n-1}$$

where W_n = width of the marginal increment (distance from the otolith growing edge to the centre of the outer-most complete opaque zone), and W_{n-1} = width of the previous complete increment (distance from the centre of the outer-most complete opaque zone to the centre of the second from outer-most opaque zone) (Tanaka *et al.*, 1981). An opaque zone was considered complete if translucent material was detectable between it and the otolith edge. The sub-sample included every fish, up to a maximum of 30 per age class, per month sampled. Widths were measured in microns using image analysis software on digitised images and were taken from the proximal growing edge, ventral to the sulcus acusticus (Fig. 2.1). Analysis of variance on arcsine transformed indices of completion was used to test for significant differences between indices of completion and month sampled (Davis and West, 1992). Mean marginal increments were plotted separately for otoliths with 2 to 12 opaque zones and pooled for otoliths with more than 12 opaque zones, against month sampled.

The timing of opaque zone formation was determined by examining the same subset of 1575 otolith sections for the presence or absence of opaque material on the same growing edge, also at 100X magnification using transmitted light.

2.2.8 Criterion for edge interpretation

The lower magnification (25X) used for the counts of opaque zones for age estimation necessitated the development of a criterion to ensure the inclusion of newly deposited opaque zones in samples collected around the time of opaque zone formation. The criterion was based on the categorization of the otolith growing edge (wide, intermediate or narrow at 25X magnification), the timing of opaque zone formation (derived from edge analysis using 100X magnification) and the designated birthdate.

2.3 Results

2.3.1 Otolith structure

The transverse, sagittal otolith sections from *Notolabrus fucicola* showed alternating zones of translucent and opaque material radiating from a uniformly opaque inner zone when viewed with transmitted light (Fig. 2.1). The two inner most opaque zones (immediately exterior to the uniformly opaque inner zone) were consistently broader than subsequent opaque zones (Fig. 2.1). Of the 2826 otoliths read, 2% were rejected due to technical failure resulting in unclear increment structure.

2.3.2 Designation of a birthdate

Mean gonado-somatic indices for both male and female *N. fucicola* peaked at around 4% in early October, indicating a peak in spawning activity in October. Back-calculated birthdates from validated daily increment counts in juvenile *N. fucicola* also suggested that October - November is the peak of spawning activity (Welsford, 2003a). To reflect this pattern, a birthdate of 1st of October was applied when estimating age. Spawning activity does, however, extend well beyond this period with individuals found in spawning condition as early as August and as late as January.

2.3.3 Precision

The APE for the within reader comparison for the primary reader (Reader A) was 0.8%, with 89% of readings in agreement and a maximum difference of 3 zones. Age bias graphs showed a high level of agreement between readings (Fig. 2.2). There was no age bias in the residuals, as no significant difference was detected between the age frequencies generated from the first and second reads using a G-test for goodness of fit ($G = 4.3$, $df = 13$, $\chi^2_{0.05} = 22.36$). All of the largest discrepancies (3 zones) and 60% of 2 zone discrepancies were from the first 300 otoliths read. Otoliths with a difference of greater than 1 zone were read a third time by the Reader A. The third readings, when compared with the second readings yielded no discrepancies of greater than 1 zone. Age estimates were derived from readings made by the Reader A and, in the case of the first 1011 otoliths, from the second readings made by the Reader A.

The APE for the between-reader comparison was 2.6% with 67% agreement and a maximum difference of 3 zones. Age bias graphs showed a high level of agreement between readers, with the exception of a small number of specimens above 12 years of age (Fig. 2.2). There was no age bias in the residuals, as no significant difference was detected between the age frequencies generated from the reads of the primary and secondary readers, using a G-test for goodness of fit ($G = 12.4$, $df = 11$, $\chi^2_{0.05} = 19.7$).

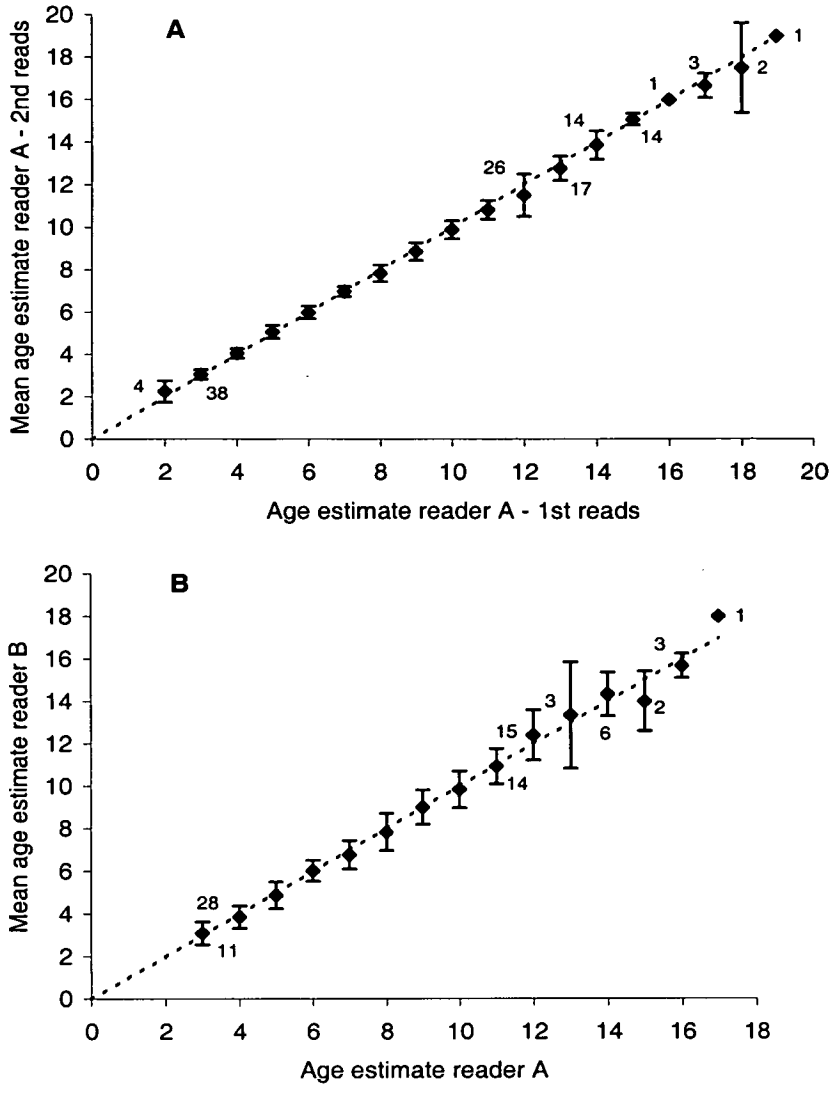

Figure 2.2: Age bias plots of mean age estimates compared to the initial reading by the primary reader. A within reader bias and B between reader bias. Value labels are sample size (when <30) and error bars are standard deviation. Dotted line indicates equal ages.

2.3.4 Validation of first annual increment

The first three opaque zones exterior to the uniformly opaque inner zone occurred at mean distances of 365 μm (SD = 25 μm, n = 100), 546 μm (SD = 33 μm, n = 100) and 691 μm (SD = 41 μm, n = 100) from the primordium, respectively (Fig. 2.1). Young of the year fish were first captured in artificial habitats in November. In March, 0+ fish had a mean transverse total otolith radius of 314 μm (SD = 86 μm, n =

9), and by May a mean of 444 μm (SD = 23 μm, n = 6) (Fig. 2.3). Young of the year fish sampled in the following October (at around 1 year of age), had a mean transverse otolith radius of 574 μm (SD = 6 μm, n = 2) (Fig. 2.3). This corresponds with the location of the second opaque zone in otoliths of adult fish indicating that the second opaque zone corresponds with the first birthday.

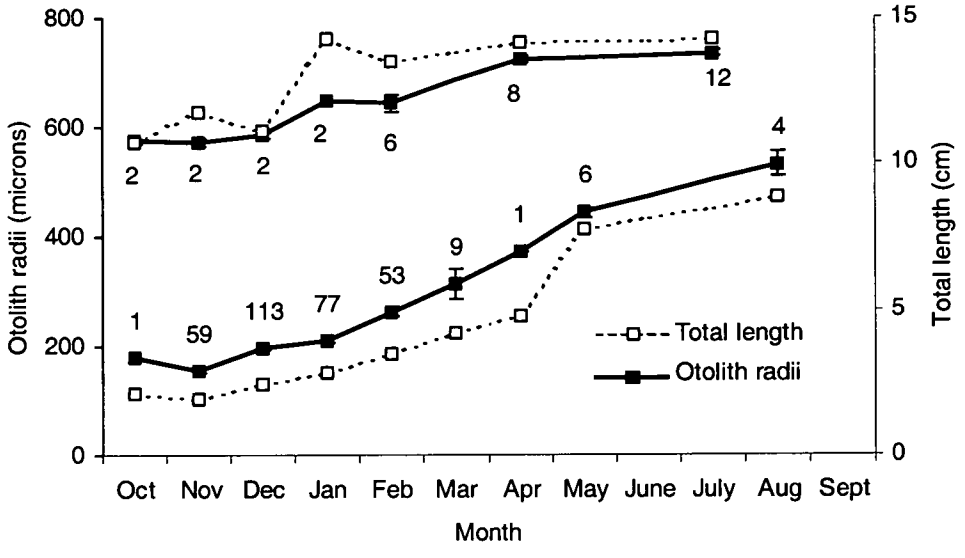

Figure 2.3: Monthly progression of mean otolith radius and mean total length of 0+ and one year old *Notolabrus fucicola*. Value labels are sample size and error bars are standard error.

2.3.5 Validation of the periodicity of increment formation

The higher magnification (100X) used for edge interpretation provided excellent clarity for the measurement of the width of the translucent margin on the otolith growing edge (Fig. 2.5). Mean indices of completion (C) peaked around October for both years of sampling and for all age classes up to 12 opaque zones (Fig. 2.4). Because there were no changes in the appearance of increments after age 8 (mean increment width 29.6 μm, SD = 6.5μm, n = 200) and due to low samples sizes, otoliths with more than 12 opaque zones were pooled for marginal increment analysis.

The pooled sample also showed peak mean C values in October for both years of sampling (Fig. 2.4). The one-way ANOVA of arcsine square-root transformed C values by month showed significant differences ($F_{8,184} = 92.3$, $P < 0.001$). Post-Hoc tests (Tukey HSD) showed fish sampled in February (the annual minima) were significantly different from fish sampled in August, September, October, November and December. Higher standard errors of mean C values for samples collected from November to January were due to increasing proportions of otoliths with a narrow zone of translucent material on their margin.

2.3.6 Timing of opaque zone formation

The 100X magnification used for the marginal increment analyses provided adequate resolution for the detection of opaque material on the otolith growing edge (Fig. 2.5). Opaque material was absent on the otolith growing edge of samples collected in January through to August and was detectable in 13.8 % of pooled age classes from samples collected in late September, 88.2 % from October, 94.7 % from November and 69.3 % from early December collected samples (Fig. 2.6). This indicates that for the period sampled, opaque zones were deposited on the sagittal otolith growing edge of *N. fucicola* from around September to December.

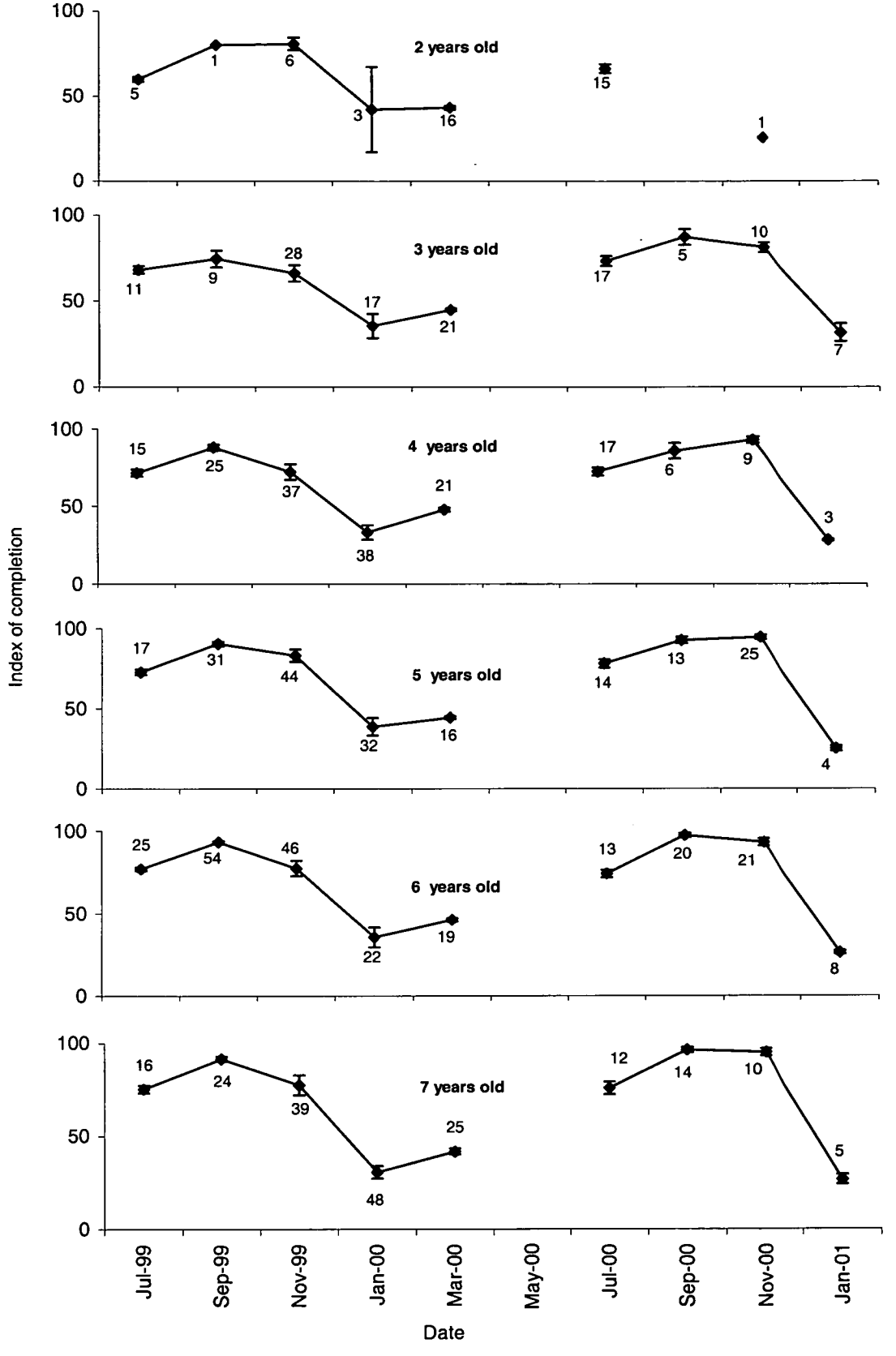

Figure 2.4: Bimonthly trends in indices of completion for sagittal otoliths of *Notolabrus fucicola*. Value labels are sample size and error bars are standard error.

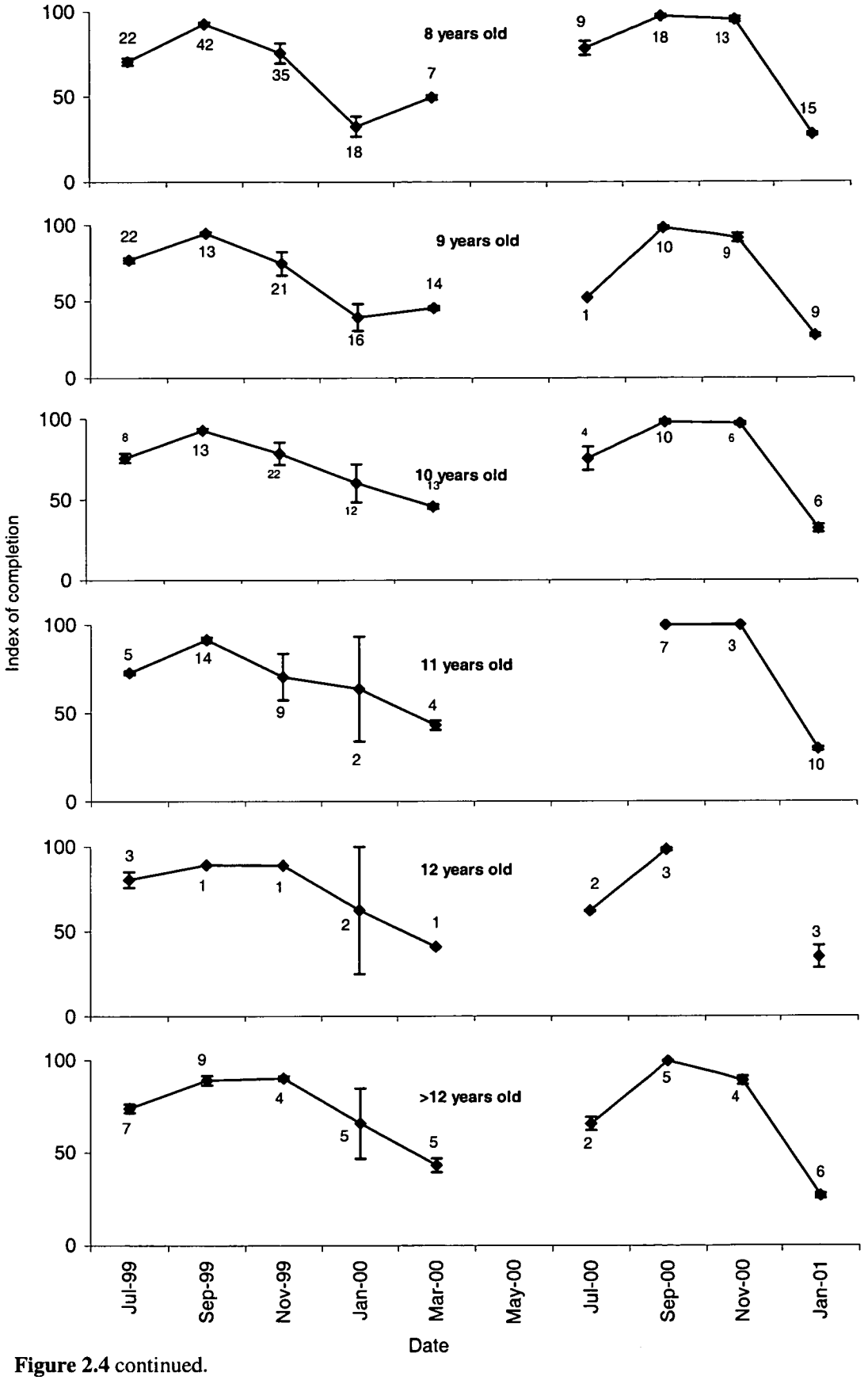

Figure 2.4 continued.

2.3.7 Criterion for edge interpretation

In contrast to higher magnification used for edge analysis, opaque material was not detectable on the otolith growing edge under the lower magnification (25X) used for counting opaque zones and the only evidence of a newly deposited opaque zone was the presence of a narrow translucent zone on the otolith growing edge. Newly formed opaque zones, despite being deposited in September to December, were undetectable at 25X magnification in November samples (all otoliths having a wide translucent margin), were first detectable in December (a small proportion otoliths having a narrow translucent margin) and were not detected in all otoliths until April samples (where every otolith had a narrow translucent margin). Thus, it was necessary to develop a criterion to ensure that newly formed opaque zones were included in the opaque zone counts taken at 25X magnification. For samples collected between October 1st (the designated birthdate and near the onset of opaque zone formation) and April 1st (the time at which all newly formed opaque zones were detected), otoliths with a wide margin (when viewed under 25X magnification) were deemed to have an unseen opaque zone on their margin (and had 1 year added to their age estimate), whilst otoliths with a narrow margin were deemed not to have an unseen opaque zone on their margin and were left unadjusted.

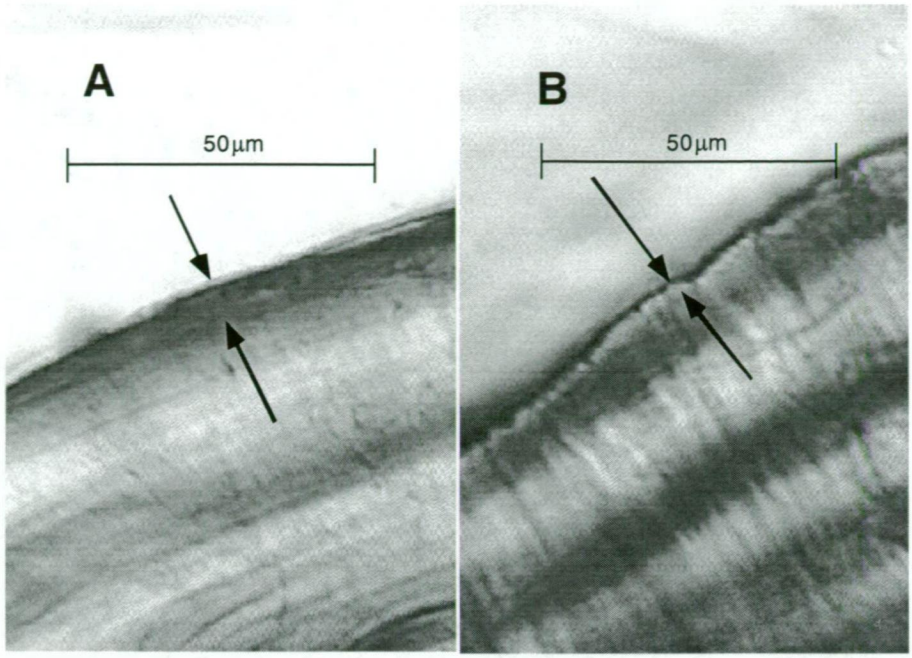

Figure 2.5: Photomicrographs of the proximal otolith growing edge (ventral to the sulcus acusticus) showing a partially deposited opaque zone (between arrows in section A, sampled in November) and a narrow translucent margin (between arrows in section B, sampled in February).

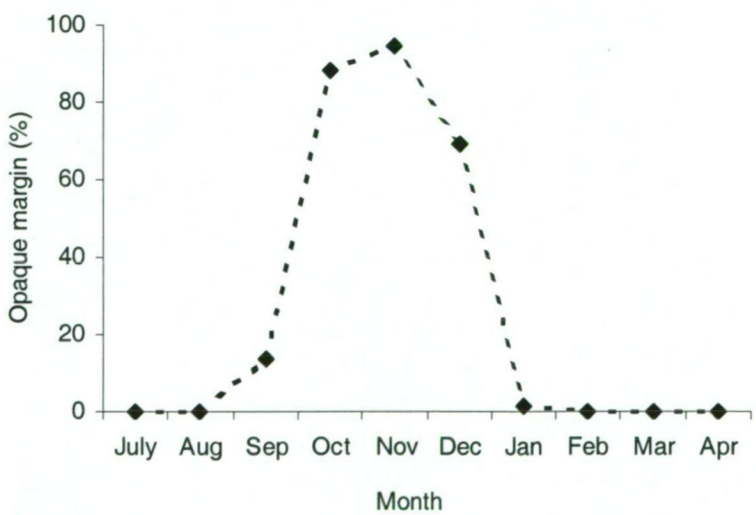

Figure 2.6: Percentage of otoliths with an opaque zone on the growing edge by month sampled.

2.4 Discussion

The transverse sectioning of *Notolabrus fucicola* sagittal otoliths provided an appropriate method for this study, with annual opaque zones readable across all age classes. This was demonstrated by the precision analyses that showed that thin sagittal sections provided reproducible age estimates of *N. fucicola*, particularly with increasing reader experience. The clarity of increment structure in sectioned otoliths was consistent with the findings for other temperate species (Francis *et al.*, 1992, Morison *et al.*, 1998).

Direct methods of establishing the position of the first annual increment in otoliths from adult fish have included counts of daily increments out to one year (Arneri *et al.*, 1997) and analysis of captive juveniles (Stewart *et al.*, 1999). However, Welsford (2003b) was only able to interpret daily rings in *N. fucicola* out to around 250 days, beyond which the increment structure became too compressed. The use of cohort structure to estimate the age of juveniles, and hence the radius at the first annuli in adults (Jordan, 2001a), whilst less direct method than the use of daily increments, can provide a robust interpretation of annuli in young fish (Campana, 2001). Given the strong cohort structure in their first 2 years (Fig. 2.3) and the low degree of dimensional variability in the inner structures in adult otoliths, *N. fucicola* are well suited for this method.

The close similarity between the mean transverse radius of sagittae from one year old *N. fucicola* (574 μm) and that of the second opaque zone in transverse otolith sections from older specimens (546 μm) confirmed that the first opaque zone (mean radius 365 μm) was deposited prior to the first birthday. Sub-annual macrostructure prior to the

first annual zone has been reported in a number of other species (Kerstan, 1995, Mann Lang and Buxton, 1996, Karlou-Riga, 2000). The presence of a clear sub-annual opaque band within the first year supports the contention that validation of an ageing methodology must include determination of the position of the first annulus (Francis *et al.*, 1992, Campana, 2001). Clearly, if this requirement were ignored in this species, fish would be over-aged by one year.

The analyses of the otolith growing edge indicated that opaque zones were deposited annually, from approximately September to December, across all age classes and over both years sampled. This timing was consistent with other studies suggesting that opaque zones are deposited in late austral spring and early summer (Fowler and Short, 1998, Choat and Axe, 1996, Cappo *et al.*, 2000). The otolith radii analysis suggested that the first annual opaque zone was deposited around October. Francis *et al.* (1992) reported that in *Pagrus auratus* opaque zones are only apparent on the margin after additional translucent material has been laid down. They stressed that it is important to distinguish between the time opaque zones become apparent and the time at which they were formed. This is consistent with the findings of this study that under low (25X) magnification opaque zones were first detected on the growing edge of otolith sections only after translucent material was deposited beyond them. Although opaque zones were detectable on the margin using higher magnification, the age estimates in this study were derived from analyses under low magnification, and thus were subject to problems of interpretation of the margin for samples collected between the time of opaque zone formation and detection. Methods of dealing with this problem range from avoiding the collection of samples around the time of annulus formation (Francis *et al.*, 1992), to the generation of algorithms to infer the presence of unseen annuli on the margin (Francis *et al.*, 1992, Fowler and Short, 1998, Cappo *et al.*, 2000, Morison

et al., 1998). The criterion developed in this study inferred the presence of unseen annuli on the basis of the margin width in the period between the beginning of October (the designated birthdate) and the following April (where the opaque zone deposited in the preceding spring was detected in all otoliths). No otoliths during this period were detected with a medium margin width and samples were processed without reference to date sampled.

The validation of the periodicity of increment formation using marginal increment analysis (MIA) has been questioned recently due primarily to the inherent subjectivity in interpretation of the otolith growing edge (Campana, 2001). In this study the use of higher magnification (100X) for otolith edge analyses and the subsequent understanding of intra-specific and temporal variation in the timing of increment formation, combined with a temperate species that displays clear increment structure right to the otolith edge, minimised this subjectivity. Campana (2001) also warned that because MIA does not utilise a measure of absolute age, it does not allow the accuracy of age estimations to be calculated. We believe that the rigorous validation protocol suggested by Campana (2001), and particularly the validation of increment periodicity for each year class from young of the year (using cohort analysis) to 12 year old fish (MIA), has provided robust age estimates in the absence of absolute ages.

The biological processes that govern the deposition of annuli in otoliths have been the source of considerable discussion (Beckman and Wilson, 1995). Annulus deposition has been related to annual migrations (Franks *et al.*, 1999, Tserpes and Tsimenides, 1995) and timing of spawning seasons (Hostetter and Munroe, 1993, Ferreira and Russ, 1994). *Notolabrus fucicola* are site attached and spawn from mid August to late

January (Barrett, 1995a), with a peak of spawning activity in early October. As the timing of opaque zone formation is not consistent with the peak of spawning activity (although there is some overlap), and as opaque zones are formed at the same time in juveniles, it is unlikely that reproductive activity directly influences the timing of opaque zone formation. The hypothesis that the stimulus for opaque zone formation may be correlated with the same external factors that initiate spawning cycles (Newman *et al.*, 1996a) is not supported by this study as spawning begins in August at least two months prior to opaque zone deposition. There is also conflicting evidence on whether opaque zones are formed at times of slow or fast somatic growth (Wilson, 1995), or in fact whether otolith growth has any direct relationship with somatic growth (Francis *et al.*, 1993). This study determined that opaque zones are deposited on the proximal edge of otoliths from September to early December. The peak growth rate for *N. fucicola* from the SE coast of Tasmania, derived from individual growth trajectories from tag release and recapture studies, occurs from November to January (Welsford, 2003a). Thus, opaque zones are deposited just prior to, and over the first month of the period of peak annual somatic growth. These findings support the hypothesis that opaque zones mark the transition from slow winter somatic growth to fast spring and summer somatic growth, rather than coinciding with periods of slow or fast somatic growth.

Otolith growth has also been linked with environmental events, particularly temperature variation (Lombarte and Lleonart, 1993, Woodbury, 1999). The timing of the opaque zone formation is also coincident with an annual increase in sea surface temperatures on the south east Tasmanian coast, from an annual mean minima of 12.6 degrees Celsius (SD = 0.44 degrees Celsius, n = 80) in August and 12.7 degrees Celsius (SD = 0.54 degrees Celsius, n = 77) in September, through an annual mean of

15.2 degrees Celsius (SD = 0.88 degrees Celsius, n = 76) in December. Thus, the timing of opaque zone formation in *N. fucicola* also supports the alternative hypothesis that otolith zonation is an independent physiological process responding to environmental stimuli (Fowler, 1995), and, rather than being linked to somatic growth, may mark the onset of increasing water temperatures that precede the summer season in southeast Tasmanian waters.

In summary, the measures taken to validate the location of the first annuli and the timing of opaque zone formation, the attention given to interpretation of the otolith growth edge and the rigorous protocol adopted have minimised the risks associated with using marginal increment analysis to validate the periodicity of increment formation and have provided robust age estimates for *N. fucicola* in eastern and south eastern Tasmanian waters. This is especially the case given the clarity of the increment structure, the consistent timing of the formation of opaque zones across all age classes and years sampled and the large sample sizes used.

Chapter 3: Spatial variation in the growth of *Notolabrus fucicola*

3.1 Introduction

Growth is one of the most important factors in determining the dynamics of fish populations (Ricker, 1975). Of the post-settlement demographic variables, growth rate is probably the most sensitive to environmental conditions and has a major influence on the size structure, size-at-maturity and hence reproductive output of reef populations (Jones, 1991).

Growth rates are sensitive to temperature (Jones, 1991) and although a positive correlation is most frequently reported(Brander, 1995, Millar *et al.*, 1999, Woodbury and Ralston, 1991, Sinclair *et al.*, 2002a, Rijnsdorp and Leeuwen, 1992), negative correlations have been reported as an adaptation to local conditions (Choat *et al.*, 2003, Yamahira and Conover, 2002). Spatial variation in diet can lead to variable patterns of growth (Jones, 1991, Kirchner and Voges, 1999), due to varying nutritional value of dietary items (Liao and Lucas, 2000). Availability of food can also have a major influence on the distribution and growth rate of a species (Jones, 1991). The characteristics of the reef habitat such as algal assemblage and reef topography also influence growth (Connell and Jones, 1991), through factors such as prey variety and density (Gillanders, 1995), and habitat availability (Tupper and Boutilier, 1995).

Growth is strongly influenced by density-dependence through mechanisms such as food-limitation (Tupper and Boutilier, 1995, Rijnsdorp and Leeuwen, 1992 , Sinclair *et al.*, 2002a, Marshall and Frank, 1999, Gust *et al.*, 2002, Peterman and Bradford, 1987). Thus, evidence of density-dependence is detectable through comparisons of

growth rates among reefs with varying ratios of population density to food resources (Barrett, 1999). This method of detecting density-dependent conditions would be particularly effective for site-attached species, as evidence of density-dependent suppression of growth rates would be preserved for longer in the absence of migration and emigration.

Populations of temperate wrasses have been found to be structured by post-settlement processes in early life through conspecific density-dependent growth suppression (Tupper and Boutilier, 1995, Jones, 1984b, Levin *et al.*, 1997). Barrett (1999) concluded that populations of the site-attached temperate wrasse *Notolabrus fucicola* on the southeast coast of Tasmania were not resource-limited, because growth rates were similar among sites with similar habitats. However, these conclusions were based on small sample sizes, the ageing methodology was unvalidated (see Chapter 2), and environmental factors likely to influence growth (such as temperature, diet or reef characteristics) were not examined among sites to ensure similarity.

The aim of this study was to produce robust estimates of growth over large spatial scales involving biologically sensible parameters and to infer the possible role of density-dependent resource-limitation through spatial comparisons of growth rates. Reef habitat characteristics, diet and sea surface temperature were also compared among sites to gauge other likely sources of variations in growth.

3.2 Materials and methods

3.2.1 Sampling

Notolabrus fucicola were collected using baited traps from Point Bailey (PB, n=643) (mid east Tasmanian coast), Eaglehawk Neck (EHN, n=610) (lower east coast), Trumpeter Bay (TB, n=819) (at the head of a large embayment on the southeast coast)

and Hen and Chicken Rocks (HCR, n=786) (southeast coast) seasonally over a period of two years (autumn 1999 to late summer 2001). Binalong Bay (BB, n=143) (upper east coast) and South Coast (SC, n=128) (far south coast) were sampled once only in austral spring 2002 (see Fig. 3.1). Fish were caught using baited fish traps set on coastal rocky reefs in less than 5 metres of water.

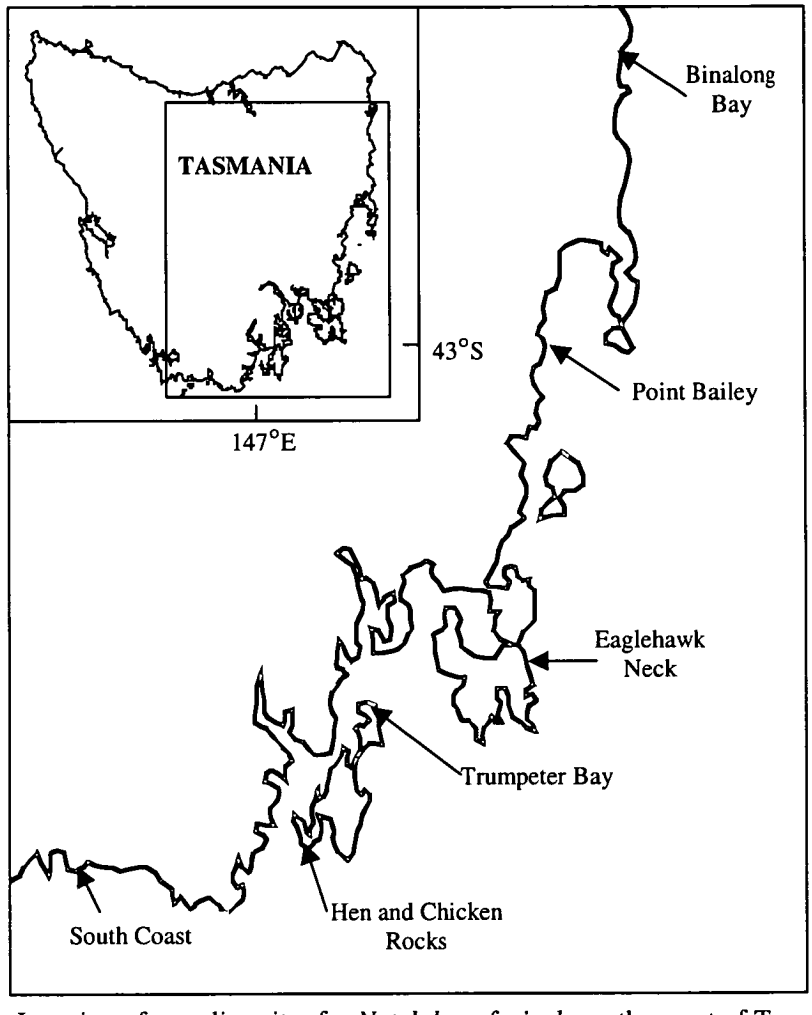

Figure 3.1: Location of sampling sites for *Notolabrus fucicola* on the coast of Tasmania, Australia.

3.2.2 Age estimation

Age estimates for the generation of growth rates were derived from transverse sectioned sagittal otoliths. Otolith processing and ageing methodologies are described in Chapter 2.

3.2.3 Growth Modelling

Growth was fitted by an appropriate mathematical function, the von Bertalanffy growth function (VBGF), to allow prediction of growth trends and facilitate comparison of growth patterns between populations. The popularity of the (VBGF) over other non-linear models (such as mathematically simpler power functions) lies in the biological relevance of the three parameters t_0 (the age at zero length), L_∞ (the theoretical mean asymptotic length) and K (the rate which L_∞ is approached). However, the VBGF was reparameterised to further increase the biological interpretability of the VBGF as t_0 and L_∞ are usually outside the range of observations and K is not a true growth rate (Cerrato, 1991). Cerrato (1991) went on to suggest that expected value parameterisations were desirable as they yield the lowest maximum parameter effects curvature but warned against basing the expected value on the maximum age in a sample. Francis's (1988) reparameterisation of the VBGF assigns three expected lengths at arbitrarily chosen ages for the parameters.

$$L_T = l_\tau + \frac{[l_\upsilon - l_\tau][1 - r^{2(T-\tau)/(\upsilon-\tau)}]}{1 - r^2}$$

where

$$r = \frac{l_\upsilon - l_\omega}{l_\omega - l_\tau}$$

The parameters l_τ, l_ω and l_υ are the mean lengths at ages τ, υ and $\omega=(\tau+\upsilon)/2$. Ages τ and υ are chosen arbitrarily from within the range of ages in the dataset (4 and 10

years respectively). Parameters were estimated by minimising squared residuals (assuming constant variation of residuals about expected length).

3.2.4 Growth comparisons

The comparison of growth rates between populations has been approached in a number of ways. Lengths at age can be compared using ANOVA (Haskard, 1992). Alternatively, growth functions can be compared directly using methods such as Analysis of Residual Sum of Squares (ARSS) (Chen *et al.*, 1992), and the likelihood ratio test (LRT) (Kimura, 1980). The LRT has the advantage of determining which parameter/s are responsible for significant differences between populations and is robust to error structures that depart from normality. The comparison of growth rates modelled with Francis' reparameterised version of the VBGF, using the LRT provides a particularly powerful methodology as the expected value parameters can be positioned at ages that maximise the biological interpretability of the comparison (such as at the age-at-maturity or at the minimum legal size limit of the fishery). Re-sampling strategies such as randomisation tests and bootstrapped confidence intervals are also used to compare growth rates between populations and, being empirically derived, are particularly useful with biased datasets (Haddon, 2001).

Initially, reparameterised VBGFs were compared pair-wise within site by sex using the LRT, to establish whether site comparisons could be conducted with the sexes pooled. Growth functions were then compared pair-wise between sites (by sex where relevant) using the LRT. Prior to each comparison, the age range was standardised between sites by removing data-points whose age group was not represented in both datasets.

Significantly different sites suspected of Type 1 error (i.e. having low level significant differences) were also compared pair-wise using a randomised version of the likelihood ratio test (Haddon, 2001), to test the assumption that the likelihood ratio adheres to the χ^2 distribution. In the randomised version, the two datasets were pooled and randomly reallocated (without replacement) 1000 times. Random reallocations were stratified by age class to ensure that the original age structures were retained in the randomised populations. For each randomisation the LRT's basecase and coincident curves constraint were used to generate a chi-square statistic. An empirical probability density function was generated for each comparison from the frequency distribution of chi-squares from the randomisations. The level of significance of differences in growth between sites was adjusted for the number of comparisons using the Bonferroni method (Sokal and Rohlf, 1995).

Bootstrap 95% confidence intervals were generated for parameter estimates by randomly resampling the dataset from each site (1000 times with replacement) and generating new parameter estimates. Resampling was stratified by age class to ensure that the original age structure was retained in the resampled population. Confidence intervals were calculated and corrected for bias arising from the difference between the observed value and the median bootstrap parameter values (Haddon, 2001). Growth rates between sexes and between sites were compared visually by plotting bootstrap parameter estimates against one another and by examining overlaps in 95% confidence intervals.

3.2.5 Dietary comparisons

Stomach contents were removed, sorted and categorised to at least class level for every fish from the four seasonally sampled sites. Dietary categories were weighed to

the nearest gram. Fish with stomach contents of more than 50% of bait (by weight) were excluded from the dietary analysis.

3.2.6 Site characteristics

Reef boundaries, macro-algal characteristics and depth profiles of the four seasonally sampled sites were determined using a differential GPS and a Furuno 600L colour echo sounder. Ground-truthing was conducted using an underwater viewer in shallow water (<5m), diver observations in medium depths (5-20m) and a submersible colour video camera (Benthos 4208 8X zoom) in deeper water (>20m). Position, depth and substrate data were imported into Arcview 3.2® to allow comparison of reef and site areas.

Weekly sea surface temperatures (SST) for whole degree blocks collected from Oct 1982 to Oct 2002 by Reynolds (from the NOAA-CIRES climate diagnostics centre, Boulder, Colorado, USA, http://www.cdc.noaa.gov) were used to estimate average SST for the vicinity of each site. SST data for the following centred blocks were used to estimate average SST; 43.5°S 146.5°E for SC, 43.5°S 147.5°E for HCR and TB, 43.5°S 148.5°E for EHN, 42.5°S 148.5°E for PB and 41.5°S 148.5°E for BB. Terrestrial temperature sources from each block have been excluded from the analysis.

3.3 Results

3.3.1 Growth comparisons

Length-at-age estimates of *Notolabrus fucicola* indicated high variability among individuals and over the range sampled were adequately described by the von

Bertalanffy growth function (VBGF) at every site. Generally growth was more variable among sites than between sexes within site.

Table 3.1: Estimates of the parameters of the reparameterised VBGF by sex and site and results from the likelihood ratio tests between sexes with sites. Probability values are with respect to the Chi square distribution ($P\chi^2$) and, where relevant, with respect to an empirical probability density function (P_{emp}) derived through randomisations of the populations compared.

Parameter	BB	PB	EHN	TB	HCR	SC
L_{4Male}	217.20	182.61	184.35	182.30	184.31	184.08
$L_{4Female}$	216.86	185.27	186.15	182.67	185.56	174.86
L_{7Male}	280.44	234.47	241.43	234.37	231.89	226.42
$L_{7Female}$	285.58	243.64	241.26	238.33	235.56	216.35
L_{10Male}	313.09	275.03	281.28	277.10	266.92	261.45
$L_{10Female}$	325.75	287.84	282.00	280.96	271.20	256.25
n_{Male}	34	243	160	351	253	49
n_{Female}	109	390	434	465	530	78
χ^2	2.72	44.49	1.01	9.61	8.90	6.9
df	4	4	4	4	4	4
$P\chi^2$	0.60	<0.001	0.80	0.047	0.06	0.14
P_{emp}		<0.001		0.051		

Comparisons of growth rates by sex within site, using the likelihood ratio test (LRT), yielded no significant differences with the exception of TB and PB (Table 3.1). Females grew significantly faster than males at TB and PB. The larger size of females was evident at 4, 7 and 10 years, with females 4.5% larger than males at 10 years at PB, and 1% larger at TB. Due to the small difference between males and females at TB (Fig. 3.2), a randomisation version of the LRT was conducted, which yielded no significant differences (Table 3.1). Bootstrap analysis of TB also showed no significant differences at TB (Table 3.2). Consequently with the exception of PB,

sexes were pooled within sites for spatial growth comparisons resulting in twenty-one pair-wise comparisons.

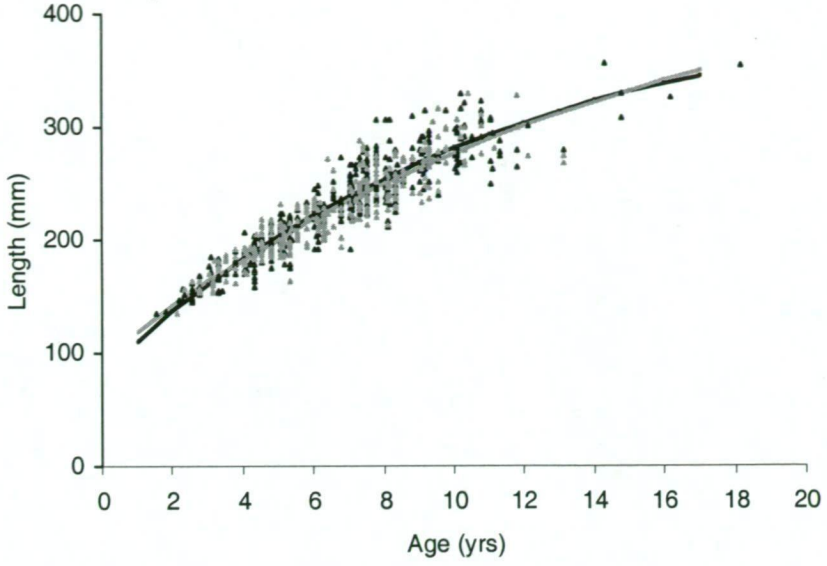

Figure 3.2. Age-at-length estimates (symbols), derived from reparameterised von Bertalanffy growth functions (lines), for *Notolabrus fucicola* sampled from TB. Black symbols are females, grey are males. Differences between growth rates were significant using the likelihood ratio test, but were not significant using randomisation tests.

Table 3.2: Estimates of the parameters of the reparameterised VBGF by site (L_4, L_7 and L_{10} = mean lengths at 4, 7, and 10 years). Sites were compared using the likelihood ratio test and are grouped accordingly (lower case letters) (α corrected using the Bonferroni method). Bias-corrected bootstrap confidence intervals are presented.

Parameter	BB	PB		EHN	TB	HCR	SC
		male	female				
LRT groups	a	b	c	cd	bd	b	e
L_4	216.9	182.6	185.2	185.9	182.3	183.4	176.2
L_{4lower}	214.7	180.6	183.7	184.0	180.9	182.0	171.2
$L_{4\ upper}$	219.2	184.6	187.0	187.9	184.0	184.8	180.4
L_7	284.3	234.5	243.6	241.0	236.7	234.2	220.4
L_{7lower}	280.7	232.1	241.5	239.1	235.0	232.9	216.1
L_{7upper}	288.1	237.0	245.8	242.9	237.5	235.8	224.8
L_{10}	323.5	275.0	287.8	281.5	279.4	270.3	259.1
$L_{10lower}$	314.20	271.8	284.8	279.7	276.2	268.5	254.0
$L_{10upper}$	330.3	278.7	291.1	284.9	280.9	272.1	264.8

Growth rates varied spatially, with size-at-age displaying a generally negative correlation with latitude. Significant differences were detected in pair-wise comparisons of reparameterised VBGFs between every site using the LRT ($\alpha = 0.0024$ adjusted using the Bonferroni method), with two exceptions. These were males at PB compared with TB and HCR and females at PB compared with EHN (Table 3.3) (Fig. 3.3). A randomisation version of the LRT between EHN and TB (the comparison with the highest potential for type 1 error due to small differences in parameter estimates between sites), no longer yielded a significant difference (Table 3.3). Size at 7 and 10 years was lowest at SC (220 and 259 mm respectively, latitude 43° 36'S) and increased with decreasing latitude from HCR (234.2 and 270.3 mm, latitude 43° 25'S), TB (236.7 and 279.4 mm, latitude 43° 9'S), EHN (241 and 281.5 mm, latitude 43° 2'S), PB females (243.6 and 287.8 mm, latitude 42° 21'S) to BB (284 and 323 mm, latitude 41° 15'S) (Table 3.3) (Fig. 3.4), with the exception of males at PB.

These findings were also supported by examination of the overlap of bias-corrected bootstrap 95% confidence intervals for the L_{10} growth parameter (Table 3.2). Bootstrap confidence intervals of L_4 and L_7 showed overlap between a number of sites, due to a convergence of growth functions at lower ages. Parameter correlation plots show a clustering of sites with similar growth rates (PB, EHN and TB) and show clear separation of BB with considerably larger size-at-age and SC with considerably smaller size-at-age (Fig. 3.4).

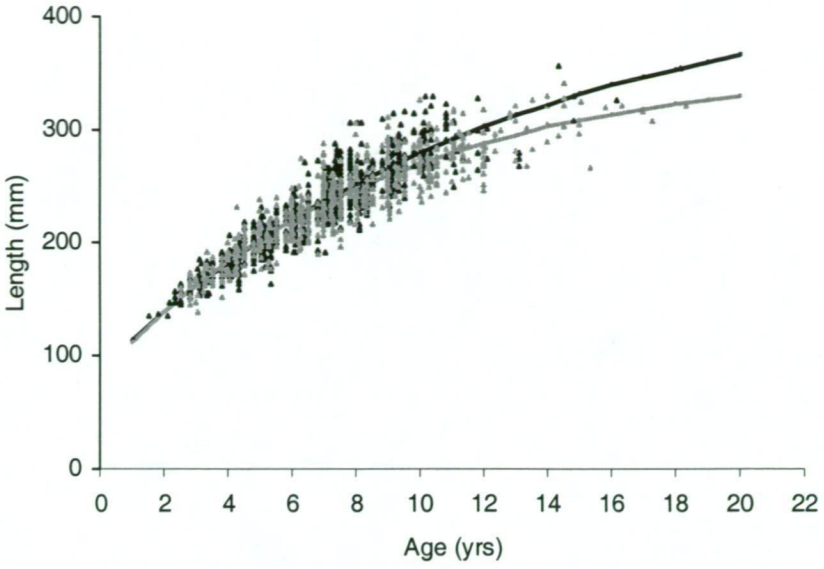

Figure 3.3: Example of a spatial comparison of growth rates that yielded significant differences. Age-at-length estimates for *Notolabrus fucicola* (symbols), derived from reparameterised von Bertalanffy growth functions (lines). Black symbols are TB, grey are HCR.

3.3.2 Diet comparisons

The phyla Annelida (class Polychaeta), Arthropoda (subphylum Crustacea, classes Malacostraca, Amphipoda and Decapoda [notably – *Plagusia chabrus*]), Mollusca (classes Gastropoda, Polyplacophora and Bivalvia [notably Mytilidae]) and Chordata (classes Ascidiacea and Osteichthyes) were represented in the diet of *N. fucicola* at every site. Small quantities of Phylum Rhodophyta present were presumably consumed incidentally when preying on grazing animals. Three primary diet items, Amphipoda, Decapoda and Bivalvia were present in large proportions at every site (Table 3.4). PB had a high proportion of bivalves (79.67% by weight) and a low proportion of amphipods (2.44% by weight) relative to the other sites.

Table 3.3: Results from the likelihood ratio tests between sites. Probability values are with respect to the Chi square distribution ($P\chi^2$, $\alpha = 0.0024$ adjusted using Bonferroni method). Where type I errors are suspected probability values are with respect to an empirical probability density function (P_{rand}) derived through randomisations of the populations compared. Probabilities in bold are comparisons where no significant differences were found.

		BB	PB		EHN	TB	HCR
			male	female			
PB male	n	386					
	χ^2	430.5					
	df	3					
	$P\chi^2$	<0.001					
PB female	n	533	633				
	χ^2	371.4	44.49				
	df	3	3				
	$P\chi^2$	<0.001	<0.001				
EHN	n	753	835	1000			
	χ^2	388.1	17.72	14.12			
	df	3	3	3			
	$P\chi^2$	<0.001	<0.001	**0.003**			
TB	n	962	1062	1209	1429		
	χ^2	627.3	5.4890	41.11	17.22		
	df	3	3	3	3		
	$P\chi^2$	<0.001	**0.14**	<0.001	<0.001		
	P_{rand}				**0.003**		
HCR	n	929	1029	1176	1396	1605	
	χ^2	627.4	10.1450	129.4	90.0589	51.74	
	df	3	3	3	3	3	
	$P\chi^2$	<0.001	**0.017**	<0.001	<0.001	<0.001	
SC	n	271	371	518	738	947	914
	χ^2	292.5	40.81	127.6	323.71	90.3642	44.02
	df	3	3	3	3	3	3
	$P\chi^2$	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001

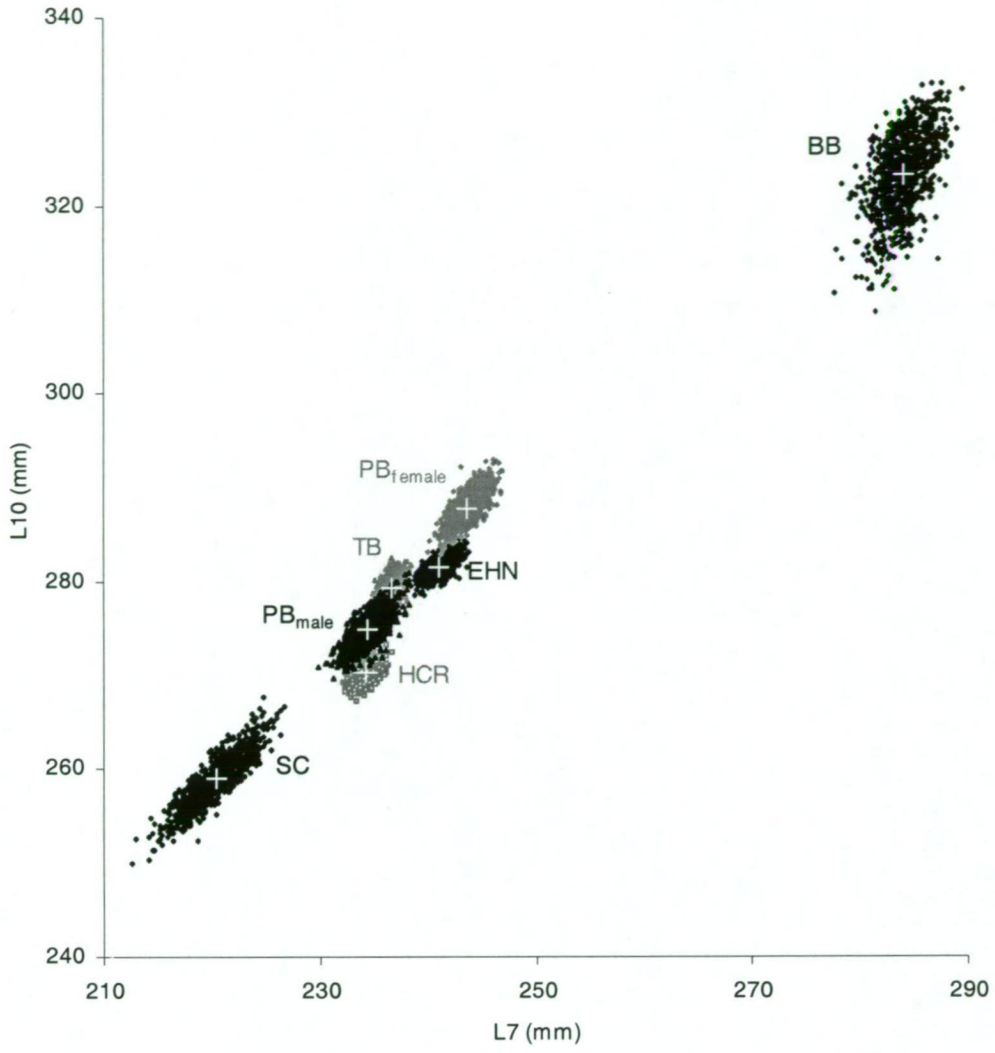

Figure 3.4: Correlation plot of parameter estimates for *N. fucicola* by site, for the reparameterised von Bertalanffy growth function parameters (white crosses) and parameter estimates generated from 1000 bootstraps (with replacement) of age-at-length data (dots).

Table 3.4: Percentage occurrence (by weight) of primary prey items by site from the stomachs of *N. fucicola* (excluding fish with stomachs containing >50% bait, by weight).

	PB	EHN	TB	HCR
Amphipoda	2.44	17.14	15.07	29.27
Decapoda	15.45	31.43	42.47	17.07
Bivalvia	79.67	38.57	38.36	52.44
n	312	180	230	194

3.3.3 Site characteristics

The reef area and depth profiles were comparable among the sites (Tables 3.5 and 3.6), but there were considerable differences in the area, continuity and depth profile of reef habitats adjacent to the sites (Figs. 3.5 a-d). Point Bailey was characterised by its position on a shallow, isolated reef associated with a short shoreline (Fig. 3.5a) (Table 3.5). Conversely, EHN, HCR and TB were characterised by their position on extensive reefs associated with long shorelines (TB had 2.3 fold greater reef area than PB, and both EHN and HCR were >4 fold larger). Eaglehawk Neck and HCR were also characterised by reef extending seaward distances of >300m and to depths of >30m.

Algal characteristics were similarly correlated with depth at each site: *Durvillaea potatorum* dominated from 0 – 5m, *Phyllospora comosa* occurred from 0 – 10m (dominating 5 – 10 m) and *Ecklonia radiata* occurred from 5 – 20 (dominating 10 – 20 m). An exception to the similarity of algal characteristics among sites was at TB where *Lessonia corrugata* occurred from 0 – 10m (dominating 5 – 10 m) and *Phyllospora comosa* was absent.

Table 3.5: Habitat characteristics of the four seasonally sampled sites.

	PB	EHN	TB	HCR
Reef profile	Low	Medium	Medium	Medium
Contiguous reef area (km^2)	0.53	2.33	1.23	2.19
Reef perimeter (km)	3.9	7.6	10.5	14.2
Sample site area (km^2)	0.11	0.10	0.07	0.07
Sample site perimeter (km)	1.9	1.32	1.8	2.2

Table 3.6: Definitions of substrate types.

Substrate	Description
Medium profile reef	Rocky substrate where relief changes regularly. Changes in depth are 1 - 4 m over short distances.
Low profile reef	Rocky substrate with little change in relief.
Patchy reef	Rocky reef elements (including boulders and rocks) intermittently outcropping from unconsolidated sediments.
Sand	Coarse grain common to highly exposed habitats

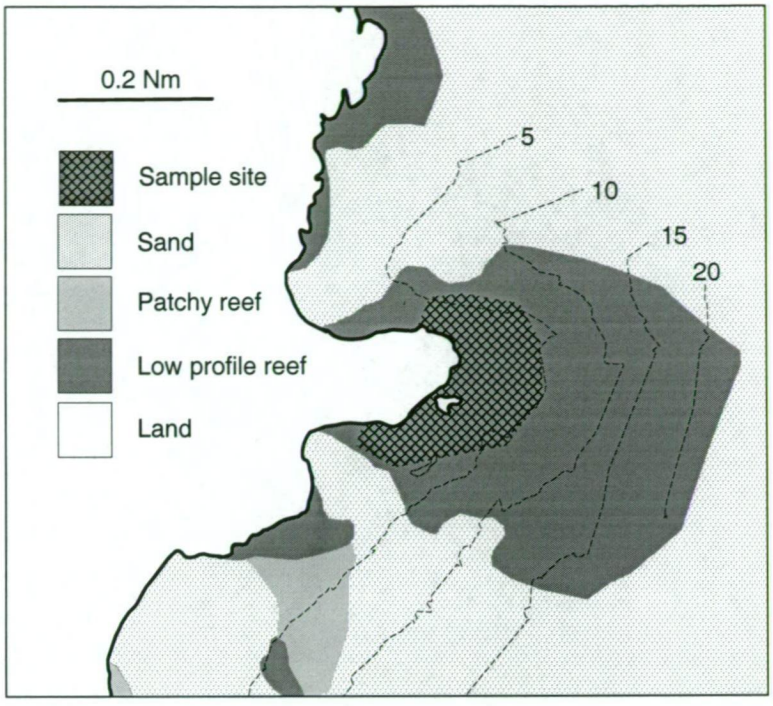

Figure 3.5 a): Habitat map of the Point Bailey sample site. Broken lines are depth contours and numbers are depths in metres.

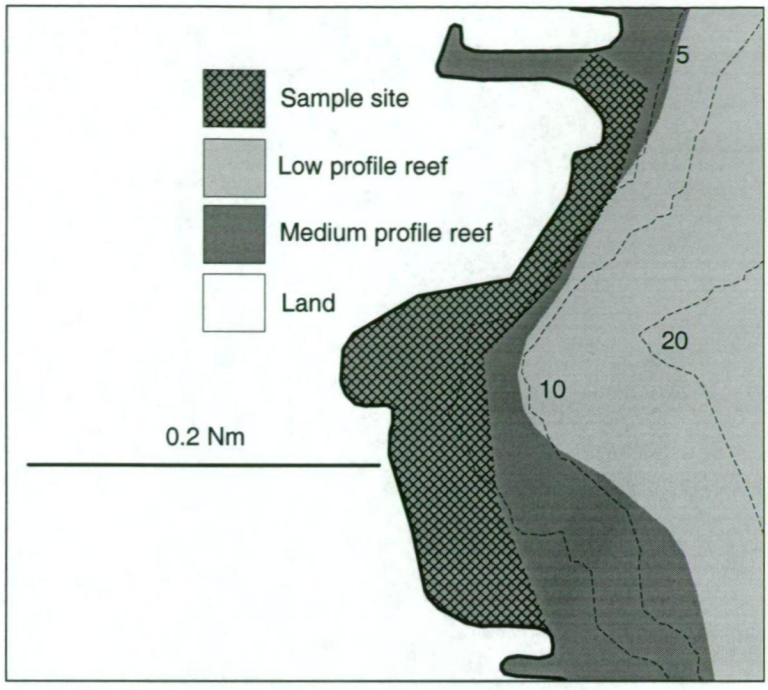

Figure 3.5 b): Habitat map of the Eaglehawk Neck sample site. Broken lines are depth contours and numbers are depths in metres.

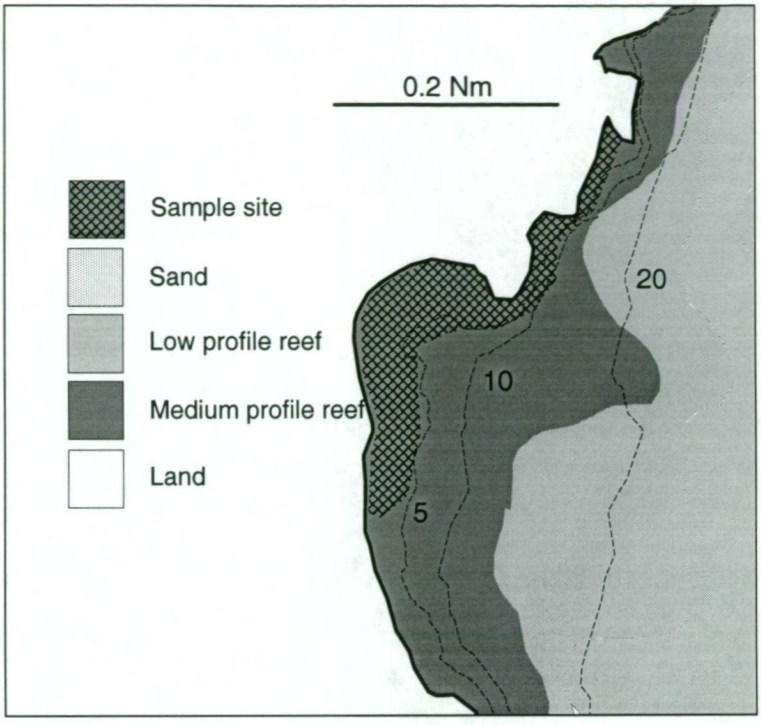

Figure 3.5 c): Habitat map of the Trumpeter Bay sample site. Broken lines are depth contours and numbers are depths in metres.

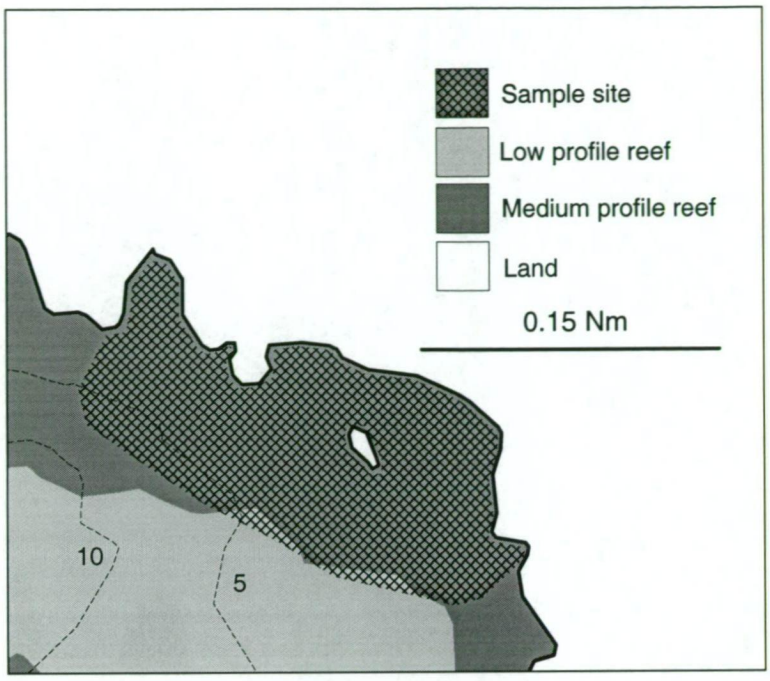

Figure 3.5 d): Habitat map of the Hen and Chicken Rocks sample site. Broken lines are depth contours and numbers are depths in metres.

Average sea surface temperatures (SST) for the one degree blocks chosen to characterise the sample sites were highest for the most northern block (adjacent to BB). Sea surface temperatures followed a trend of decreasing temperature with increasing latitude down the east coast of Tasmania to the block adjacent to EHN and followed a trend of decreasing temperature with decreasing longitude across the south of Tasmania to a minimum in the block adjacent to SC (Table 3.7).

Table 3.7: Average sea surface temperatures (SST) for whole degree blocks chosen to characterise water temperatures at sample sites. Terrestrial components of blocks are excluded from averages. Averages derived from remote sensing data.

Block centre	Site/s	Average SST (°C)	n	SE
41.5°S 148.5°E	BB	15.42	1088	1.94
42.5°S 148.5°E	PB	14.83	1089	1.77
43.5°S 148.5°E	EHN	14.04	1089	1.59
43.5°S 147.5°E	HCR and TB	13.61	1089	1.57
43.5°S 146.5°E	SC	13.35	1089	1.55

3.4 Discussion

Comparisons of growth rates between populations were conducted using both the standard and a randomised versions of the likelihood ratio test (LRT) (Kimura, 1980, Haddon, 2001) and bootstrapped confidence intervals (CI) of parameter estimates (Haddon, 2001). The LRT was the most sensitive method used as it detected statistically significant differences in more comparisons than the other methods (including every comparison where significant differences were found by the other methods). In every comparison the randomised LRT generated a higher probability than the standard LRT, however the statistical significance of the result only changed

for two comparisons; the within site sex comparison at TB and the site comparison between TB and EHN. The difference between the outputs of the theoretical LRT and the randomised LRT imply that the likelihood ratio does not conform to the Chi squared distribution due to biases in the sample data and suggests a higher risk of type I errors. This risk was exacerbated by correlation between growth parameters (observable in the bootstrap parameter plots Fig. 3.4) and by increased statistical power from the large sample sizes. The former caused increased sensitivity of the LRT (Welsford, 2003a). The most obvious example of over-sensitivity in the theoretical LRT, was the comparison by sex at the TB site, where, despite size at 10 years differing by only 1% and visual examination of growth functions revealing close similarity (Fig. 3.2), significant differences were detected.

Comparisons of the bootstrapped 95% CI of parameter estimates for L_{10} yielded the same pattern of statistically significant results as the LRT or, where relevant, the randomised LRT. Comparisons of the CI for L_4 and L_7 were less interpretable due to the lack of divergence between growth functions at earlier ages, which was also indicated by the LRT results (i.e. L_{10} was the parameter responsible for differences in every comparison that yielded significant differences). The scatter plots of the bootstrapped CI clearly showed the overlap between the sites where no differences were found and gave an easily interpretable image of the clustering of sites with similar growth rates. Hence, the empirically derived statistics provided results that were more biologically interpretable due to the reduced sensitivity of the randomised version of the LRT. Moreover, the bootstrap parameter estimates plots provided a useful way of empirically examining differences in the growth parameter differences and of visually examining the behaviour of the growth model, such as correlations between parameters (Welsford, 2003a).

There were no differences in growth rate between the sexes at each site, with the exception of the PB site where females reached a larger size more quickly than males. Feeding behaviour of *N. fucicola* has been observed to decrease at the onset of reproductive activity (Denny and Schiel, 2001). The PB site is positioned within a small sand-locked reef of a generally low geographic profile, with a very short shoreline. In contrast, the other sites are situated on larger reefs of a higher geographic profile and an extensive shoreline. Underwater observations of *N. fucicola* during the spawning season reported males devoting less time to foraging for food and more time to searching for mating opportunities than females (Barrett, 1995b). A plausible explanation for the lower growth rate in males at the PB site is that they devote relatively more time to reproductive activities than males at other sites, due to factors relating to the size of the reef.

Growth rates were found to vary between sites, with fish from BB having the highest values for all three of the parameters of the reparameterised VBGF. Parameter estimates for L_{10} decreased with increasing latitude (with the exception of males at PB) to SC where estimates were the lowest for all three parameters. Males at PB yielded growth rates similar to HCR. Growth rates were similar at TB and EHN (no significant differences) and the parameter correlation plots clearly showed a group of sites with similar growth rates (PB, EHN, TB and HCR) as separate from faster growth at the most northern site (BB) and slower growth at the most southern site (SC). Whilst growth follows a latitudinal gradient (with the exception of males at PB), and the sites clustered at similar latitudes share similar growth rates, there are physical and biological parameters that differ between sites that are more likely to have a direct effect on growth rates.

The dietary inventory of *N. fucicola* on the east and southeastern coasts of Tasmania is consistent with other temperate wrasses (Denny and Schiel, 2001, Sayer *et al.*, 1996). However, spatial differences in growth rates do not appear to be explained by differences in the relative proportions of diet items. Despite sharing similar growth rates, the diet at PB was predominantly bivalves with a low proportion of amphipods in contrast with EHN where the proportions of amphipods were much higher and bivalves much lower. The differences in diet do, however, correspond with differences in the structure of the reefs sampled. As a smaller and lower profile reef, PB may not support the same degree of diversity of prey items, or may experience wider temporal fluctuations in the abundance of prey items (Gillanders, 1995, Denny and Schiel, 2001).

Reef structure and algal assemblages differed between the sites sampled. The PB site (a smaller low profile reef) had similar growth rates to EHN (in the case of females) and TB and HCR (in the case of males) that were sited on more extensive higher profile reefs. The TB site, where *Lessonia corrugata* dominated the 5-10m depth range, had similar growth rates to other sites where *Phyllospora comosa* dominated that range. The HCR site shared similar reef extent, profile and algal assemblage with EHN, yet had significantly lower growth rates. Spatial differences in growth rates do not appear to be explained by variation in reef structure and algal assemblage, however, the only site yielding sex differences in growth (PB) also displayed markedly different reef structure.

Although *N. fucicola* live out their life on an individual reef, variation in growth is unlikely to be the result of genetically variation due to the high potential for larval

transport. Larval transport is facilitated by a dispersive pelagic phase (five to ten weeks), an extended spawning period (August to January) (Welsford, 2003a) and highly variable coastal hydrography (Bruce *et al.*, 2001, Harris *et al.*, 1987). Furthermore, Ward (2001) found limited genetic differentiation in fish sampled over a larger spatial scale than this study, due to influential currents and a lack of major oceanographic and environmental barriers to gene flow in the south eastern region of Australia.

The sea surface temperature (SST) data indicated a general trend of decreasing temperature down the east coast and across the south coast of Tasmania and is consistent with the decreasing influence of warm water from the East Australian Current (EAC). Spatial variation in growth rates is consistent with the trend in water temperatures with high growth rates in warmer water in the north east of Tasmania through to slow growth rates in the colder waters of the south coast of Tasmania. A positive relationship between water temperature and growth rates of fish is well documented (Sinclair *et al.*, 2002a, Brander, 1995, Woodbury and Ralston, 1991, Millar *et al.*, 1999).

In summary, the biological relevance of the parameters in Francis' reparameterised VBGF provided interpretable growth models for the purposes of comparisons of growth rates. The difference between results of statistical significance from the LRT and results from empirically derived tests (the randomised version of the LRT and the bootstrap CI of the parameter estimates) suggested that the data violated the assumption that the likelihood ratio adheres to the χ^2 distribution and increased the potential for type I errors. However, the risk of Type I errors were minimised by the

low α value (due to the Bonferroni correction used to account for twenty one dependant comparisons) and the use of empirically derived tests (particularly for comparisons with low level significant differences). The combination of the biological relevance of the parameters, the conservatism of the empirically derived bootstrapped CIs and their visual interpretability when plotted, provided a powerful method of comparing growth rates. Growth was found to vary spatially and followed a trend of decreasing growth rates with decreasing water temperature and increasing latitude.

Chapter 4: Size-related biases in samples of *Notolabrus fucicola* trap caught from populations exposed to fishing mortality

4.1 Introduction

Methods used to collect samples of fish are commonly subject to size-related biases. Observational surveys are biased towards detection of larger, more conspicuous individuals while fishing gear used to collect samples will rarely sample all size classes equally (Ricker, 1975). The size-selectivity of fishing gear refers to the proportion of the population retained as a function of fish size and is determined by the mechanics of the gear (eg. mesh size) and the morphometric and size-specific behavioural characteristics of the fish (Anganuzzi *et al.*, 1994, Millar, 2000). However, other factors such as season (Ziegler *et al.*, 2002), habitat and depth (Cui *et al.*, 2001), soak time and intra and inter-specific interactions (Miller, 1990) can also influence the size-selectivity of a particular fishing method. Whilst size-selectivity is a dominant influence on catchability within a population, other factors such as sex-related behavioural interactions during spawning season can also structure catches (Ziegler *et al.*, 2002).

Size-selectivity is usually derived indirectly from trends in the size structure of catches from a single population fished with gears of varying selectivities (Cui *et al.*, 2001, Hovgard, 1996, Santos *et al.*, 1995, Stewart and Ferrell, 2003, Xu and Millar, 1993). However, such methods are based on the often erroneous assumption that the relative efficiency of capture of the most highly selected size class is constant across gears of varying size-selectivities (Jensen and Hesthagen, 1996). More robust methods calculate selectivity directly using captures from a population of known size

structure (Jensen and Hesthagen, 1996) or comparatively from mark recovery experiments (Finstad *et al.*, 2000, Anganuzzi *et al.*, 1994, Myers and Hoenig, 1997).

Selectivity is usually described parametrically using unimodal curves such as normal, skewed normal, log-normal or gamma distributions for gill nets and non-decreasing monotone curves such as the logistic distribution for towed gear and traps (Hovgard *et al.*, 1999, Millar and Fryer, 1999). Selectivity curve parameters are usually fitted estimated using least squares (Millar, 1995) or maximum likelihoods with binomial error structure (Kirkwood and Walker, 1986, Millar and Holst, 1997) estimation methods (Millar and Fryer, 1999, Myers and Hoenig, 1997). Gear selectivity is primarily used to correct the size structure of a sample to reflect that of the sampled population and can also be applied to age structure (Finstad *et al.*, 2000).

Baited traps are routinely used in commercial fisheries to target fish in both tropical and temperate waters and on both reef and soft sediment habitats (Gobert, 1998, Whitelaw *et al.*, 1991, Mahon and Hunte, 2001, Newman and Williams, 1995). Baited traps have also been utilised to collect samples for research, though primarily for invertebrate species (Recksiek *et al.*, 1991). Although selectivity of traps has been studied extensively for invertebrate species (Xu and Millar, 1993, Ziegler *et al.*, 2002, Frusher and Hoenig, 2001), the research has been focussed on improving catch rates of targeted species (or sizes) and eliminating unwanted by-catch or unwanted undersize fish (Whitelaw *et al.*, 1991, Recksiek *et al.*, 1991, Gobert, 1998, Newman and Williams, 1995). No research to date has utilised direct methods of calculating the selectivity of fish traps for the purpose of correcting size-related biases in fishery-independent catches, allowing robust estimation of population parameters.

Size-selective fishing mortality can have dramatic effects on the population structure of fished communities and the nature and extent of such effects is dependent on the dynamics of the fishery and the sizes targeted in relation to the ecology of the species. Similarly, size-selective-fishing mortality can dramatically bias population parameters such as growth and age structure that are derived from samples taken from fished populations. Practically all fisheries have a component of size-selectivity that structure catches. These may be regulatory such as minimum legal size limits (LSL), market-driven, governed by the selectivity of the fishing gear and/or dependent on trends in vulnerability to capture over the life history of the exploited species.

Size-selective fishing mortality in fisheries limited by a minimum legal size limit (LSL) removes faster growing individuals first. Consequently, growth rates determined from commercial catches may be overestimated. Conversely, fishery-independent studies have shown that fishing reduces the mean length-at-age in targeted size classes and particularly in size classes around the LSL (Weinberg and Helser, 1996, Smith *et al.*, 1990, Lucena and O'Brien, 2001, Sinclair *et al.*, 2002a). The extent that size-selective mortality biases the estimated growth rate of exploited species is influenced by the extent of variation of size-at-age (particularly around the LSL) and the rate of onset of fishing mortality at the LSL (Sinclair *et al.*, 2002b). For example, knife-edged fishing mortality at the LSL of a species with high variation of size-at-age will have a greater potential for size-selective removal of faster growing fish from the age classes approaching the fishery, resulting in lower size-at-age in those age classes remaining in the population, which will distortion growth estimates. Clearly, this is a particularly important consideration when comparing growth rates of populations subject to varying or unknown degrees of fishing mortality.

The impact of this bias on estimates of growth rates can be investigated through examination of fishing mortality at the LSL. Size-selective biases (such as size-selective fishing mortality) can violate the assumptions of traditional methods of parameter estimation (i.e. normality and constant variation of residuals), as the minimum targeted size is approached. Thus, the magnitude of this bias can be assessed through examination of the effects on growth parameters of manipulations of the error structure of the growth model fitted.

Populations of *Notolabrus fucicola* sampled in this study were all from areas susceptible to commercial fishing mortality. The wrasse fishery in Tasmania exports fish live and harvests approximately 80 tonnes per year using hook and line and baited fish traps. Fishing effort is regulated through input controls including a LSL. A high proportion of the total catch is taken from the east and southeast coasts of Tasmania where catches are dominated by *N. fucicola* (Lyle and Hodgson, 2001). Fishery-dependant catch and effort data (Lyle and Hodgson, 2001) reports a variation in catches between the regions sampled in this study (see Fig. 2.1), however, these data are at a spatial scale that would include many individual reefs. As *N. fucicola* are site attached, fishing mortality may vary considerably on a local scale, and mortality on individual reefs may bear no relation to trends in regional catch statistics. Consequently, the sites sampled for this study were considered to be subject to varying and unknown levels of fishing mortality.

The aims of this study were to address size-selective biases in the *Notolabrus fucicola* age and growth dataset to allow robust comparisons of growth rates (see Chapter 3) and generation and comparison of representative age structures (see Chapter 5). A simulated fish-down combined with tagging generated a population of known size

structure on an isolated reef. This population was fished with the traps used for the age and growth dataset to allow the generation of a selectivity function for that gear. The relative influence of fishing mortality in structuring the populations sampled was investigated through comparisons of selectivity-corrected size structures and estimates of instantaneous mortality. The influence of size-selective fishing mortality on growth modelling was examined by comparing growth function parameter estimates derived using different error structures. The influence of reproductive status on the size-selectivity of the traps was investigated by examining the sex ratios in catches and through examination of sex specific size structures in catches.

4.2 Materials and methods

4.2.1 Size-selectivity of the fishing gear

Notolabrus fucicola were captured using six baited traps set concurrently on a small sand-locked reef (Fig. 4.1) at Point Bailey on the east coast of Tasmania (see Fig. 3.1) in March 2001. Traps were identical (Fig. 4.2) and deployed haphazardly over the entire extent of the reef. They were baited with 500 grams of abalone guts at each deployment and retrieved, emptied, baited and re-deployed every 90 minutes, during daylight, for five consecutive trapping days (a total of 90 trap hauls). For the first four trapping days, every untagged fish that was captured had its fork length (FL) recorded (mm), was marked with a uniquely numbered Hallprint T-bar tag inserted in the flesh adjacent to the soft dorsal fin. The third dorsal spine was removed in order to determine tag loss. The girth was recorded for a random subsample of fish (n = 50) to assess the relationship between trap mesh size, trap entrance size and size structure of catches.

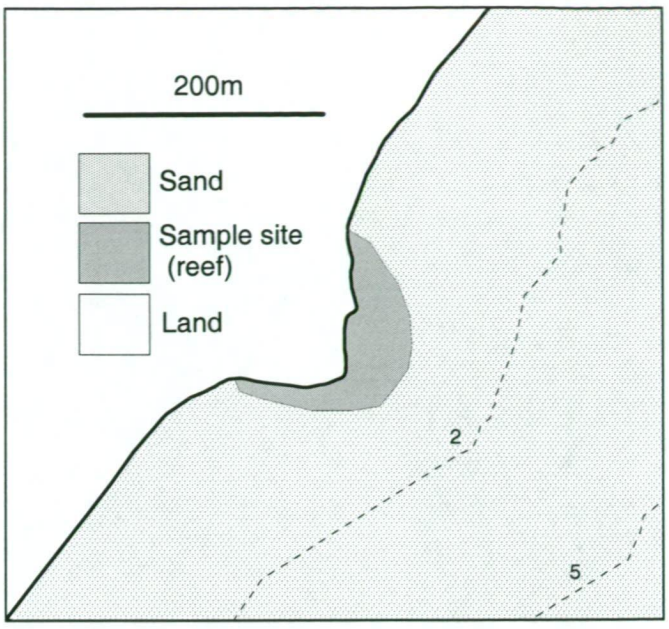

Figure 4.1: Habitat map of the Point Bailey sample site on the east coast of Tasmania used for the mark-recapture selectivity trial, showing the isolated nature of the reef. Dashed contours are depth in meters. The area of the reef sampled was 0.013 km.

On recapture of a marked fish, tag number was recorded and fish were returned to the water in the same location. If a tag loss was detected (missing third dorsal spine but no tag), fork length was recorded and the individual was retagged and returned to the water. On the fifth and final trapping day, recaptures were recorded but no fish were marked.

Losses of fish from the tagged population through natural and fishing mortality were assumed to be negligible because the sampling was conducted over a short period of time during which no other fishing activity was observed on the reef. Losses of fish through emigration were also assumed to be negligible because *N. fucicola* are site attached (Barrett, 1995b), and rarely appear to venture over unvegetated habitat

(personal observation). Also, no tagged *N. fucicola* were encountered on the nearest reef during subsequent sampling for another research program.

A selectivity index was calculated for each 20 mm size class as the proportion of the tagged population (by size class) that was recaptured on the fifth trapping day. Selectivity indices were rescaled such that the selectivity in the modal size class was equal to one. A selectivity function was generated by fitting the selectivity indices to the symmetrical logistic function;

$$r(l) = \frac{e^{(a+bl)}}{1+e^{(a+b(l)}}$$

where $r(l)$ is the probability that a fish of size l will be captured and retained. The parameters a and b are estimated such that $a < 0$ and $b > 0$.

The length at 50% retention (l_{50}) is given by;

$$l_{50} = \frac{-a}{b}$$

The Richards curve, an asymmetrical logistic function (Stewart and Ferrell, 2003) was also fitted;

$$r(l) = \left(\frac{e^{(a+bl)}}{1+e^{(a+b(l)}} \right)^{1/\delta}$$

where δ quantifies the degree of asymmetry. The parameters a, b and (in the case of the Richards curve) δ were fitted by maximising log likelihoods (with binomial error structure). The two logistic models were tested for difference using the likelihood ratio test with significant differences accepted at $\alpha = 0.05$.

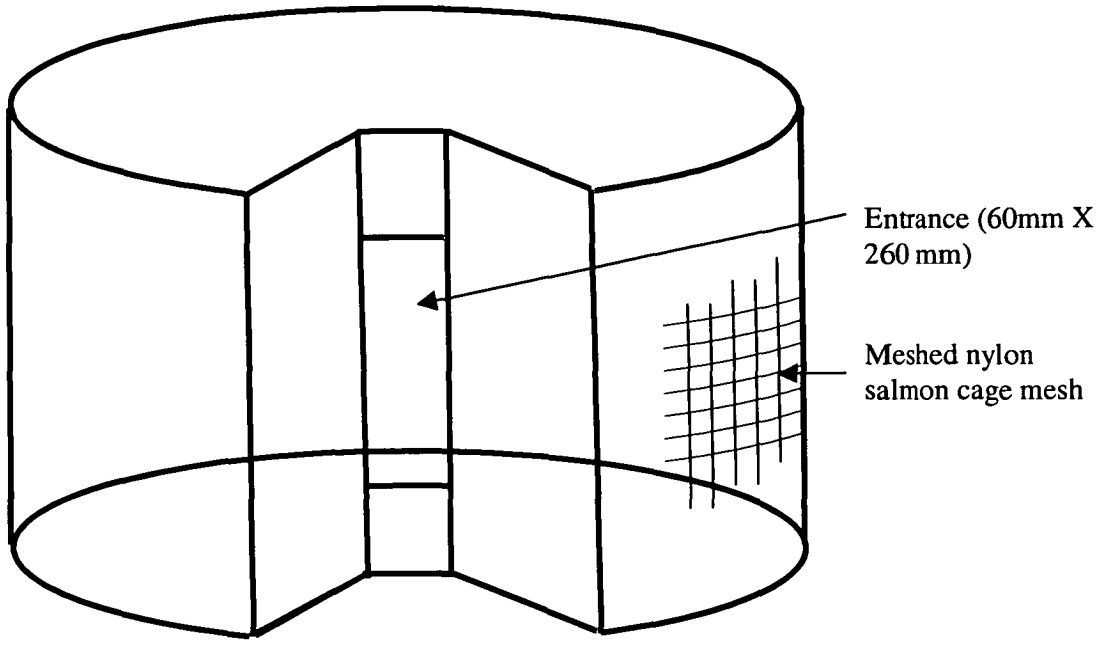

Figure 4.2: Fish traps used to collect samples of *N. fucicola*. Bait was suspended in a mesh bait sock in the middle of the trap adjacent to the entrance. Trap rigid structure was 780 mm in diameter by 470 mm in height and was constructed of mild steel rod (12 mm diameter). Traps were meshed with nylon salmon cage mesh (54 ply, 15 X 15 mm mesh). Traps were buoyed and hauled from a point above the entrance to minimise the likelihood of fish escaping through the entrance during retrieval.

4.2.2 Inference of fishing mortality from selectivity-corrected size structure and instantaneous mortality estimates

The selectivity function was used to reconstruct size structures of catches for the sites used for comparisons of age composition in Chapter 5 [i.e. Binalong Bay (BB), Point Bailey (PB), Eaglehawk Neck (EHN), Trumpeter Bay (TB), Hen and Chicken Rocks (HCR) and South Coast (SC) (see Fig. 3.1)]. Each individual was weighted by the inverse of the selectivity predicted by its length. Selectivity-corrected size and age structures were generated using the sum of the weightings for each class. Selectivity-corrected size structures were compared between sites to examine the relative impact of fishing mortality at the minimum legal size limit. The selectivity-corrected age

structures were used to generate estimates of instantaneous mortality for post-modal age classes up to and including the first age class with a corresponding mean length greater than the minimum legal size limit (t_{LSL}) (i.e. mortality prior to exposure to the fishery). The relative degree of fishing mortality was examined by site by comparing estimates of instantaneous mortality. Instantaneous mortality estimates were also compared by site with natural mortality generated from Hoenig's equation;

$$M = e^{1.46-1.01(\log_e L_\infty)}$$

where M = natural mortality and L_∞ = mean asymptotic length from the Von Bertalanffy growth model (Hoenig and Lawing, 1983).

4.2.3 Influence of size-selective fishing mortality on growth parameter estimates

The length-at-age data for each population used for spatial comparisons of growth in Chapter 3 [i.e. Point Bailey male (PBm), Point Bailey female (PBf), BB, EHN, TB, HCR and SC (see Fig. 3.1)] were examined for evidence of fishing mortality biases to growth parameter estimation.

Age-at-length data was fitted to Francis' (1988) re-parameterisation of the von Bertalanffy growth function (VBGF).

$$L_T = l_\tau + \frac{[l_\upsilon - l_\tau][1 - r^{2(T-\tau)/(\upsilon-\tau)}]}{1 - r^2}$$

where: L_T is the length at age T and $r = \frac{l_\upsilon - l_\omega}{l_\omega - l_\tau}$

The parameters l_τ, l_ω and l_υ are the mean lengths at ages τ, υ and $\omega=(\tau+\upsilon)/2$. Ages τ and υ are chosen arbitrarily from within the range of ages in the dataset (4 and 10 years respectively). Parameters were estimated firstly by minimising squared

residuals (assuming constant variation of residuals about expected length and normally distributed residuals), and secondly, by maximising log likelihoods (assuming constant coefficient of variation and normally distributed residuals). The constant coefficient of variation of residuals allows larger individuals more variation of size-at-age and effectively reduces their influence over curve fit.

Growth functions within site, but between parameter estimation methods, were compared using the bootstrap 95% confidence intervals of the growth parameters. Bootstrap confidence intervals were generated by random re-sampling (1000 times with replacement). Re-sampling was stratified by age class to ensure that the original age structure was retained in the re-sampled population. Confidence intervals were calculated and corrected for bias arising from the difference between the observed value and the median bootstrap parameter values (Haddon, 2001).

The error structure of the growth models for each population were examined to look for size-based biases that may affect parameter estimation. The residuals plots for parameter estimates assuming constant variation were compared with those assuming constant coefficient of variation for each site to assess the extent of size-based biases in the data.

4.2.4 Sex structure in catches

The role of reproductive status in the selectivity of *N. fucicola* was investigated through comparisons of sex ratios and size compositions for seasonally sampled sites (i.e. PB, EHN, TB and HCR). *Notolabrus fucicola* is a gonochoristic species with unitary sex ratios reported in populations sampled in Tasmania (Barrett, 1995a). To gauge the role of reproductive status in structuring catches, the departure from unity

in sex ratios was tested using the chi-squared test for samples collected during the spawning season (late August to early January) (Barrett, 1995a). These were compared with chi-squared tests of sex ratios from samples collected outside the spawning season. The influence of sex ratio on size-selectivity was assessed by comparisons of size structure by sex within site using the Kolmogorov Smirnoff two-sample test.

4.3 Results

4.3.1 Size-selectivity of the fishing gear

Catches of untagged *Notolabrus fucicola* declined sharply from the first trapping day (250 fish tagged over 24 trap deployments). A total of 315 fish were tagged during the course of the study. Only three tag losses were detected and, being from highly selected size classes (210, 250 and 270 mm), were not considered to compromise the analysis. The smallest size class encountered in the traps was 130 mm and the largest was 350 mm. Each size class was well represented in catches with the exception of small numbers of fish above 300 mm FL (the minimum legal size limit of the fishery) which contributed less than 4% of tagged fish (Fig. 4.3). On the last trapping day 86 tagged fish were recaptured (>80% of the total catch for that day) from 18 trap sets (Fig. 4.4). Also on the last fishing day, the total catch per trap did not exceed 10 fish and every trap retrieved had bait remaining.

Selectivity increased with size to a maximum in the 270 mm size class, declined slightly at 290 mm, after which it declined sharply before rising at the maximum size class (Fig. 4.3). The maximum girth measured, 52 mm (which at 354 mm FL, was also the largest fish tagged) was still 10 mm narrower than the trap entrance. The

minimum girth measured, 20 mm (which at 135 mm FL was the smallest fish tagged) was 5 mm larger than the trap mesh size (15 mm).

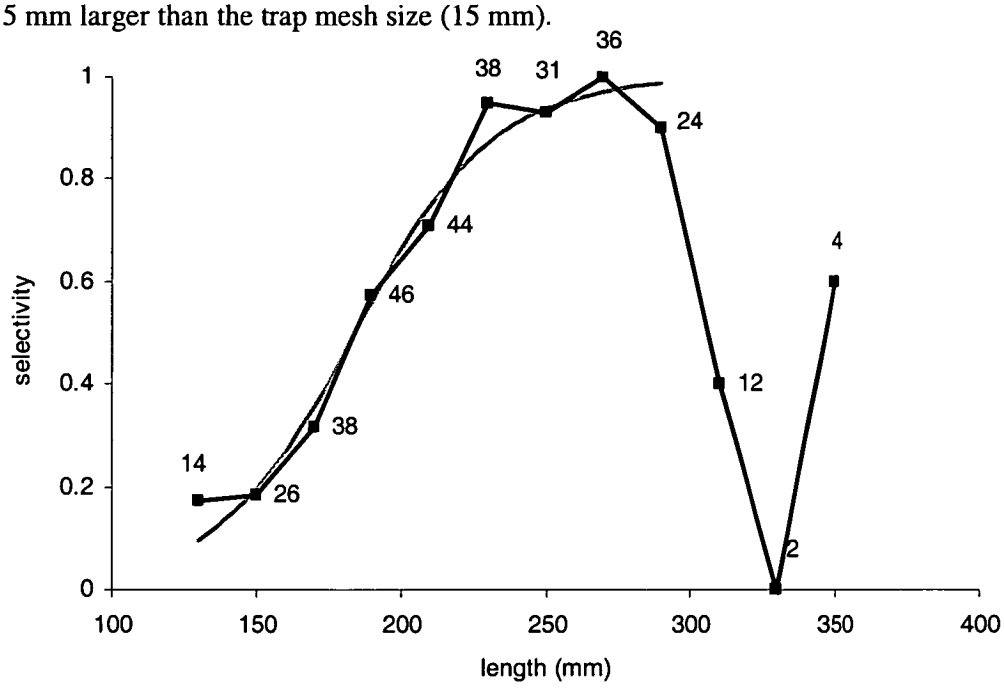

Figure 4.3: Selectivity indices by size class for trap caught *N. fucicola* (black symbols) and the logistic selectivity function (grey line). Data labels are the number of fish tagged in each size class.

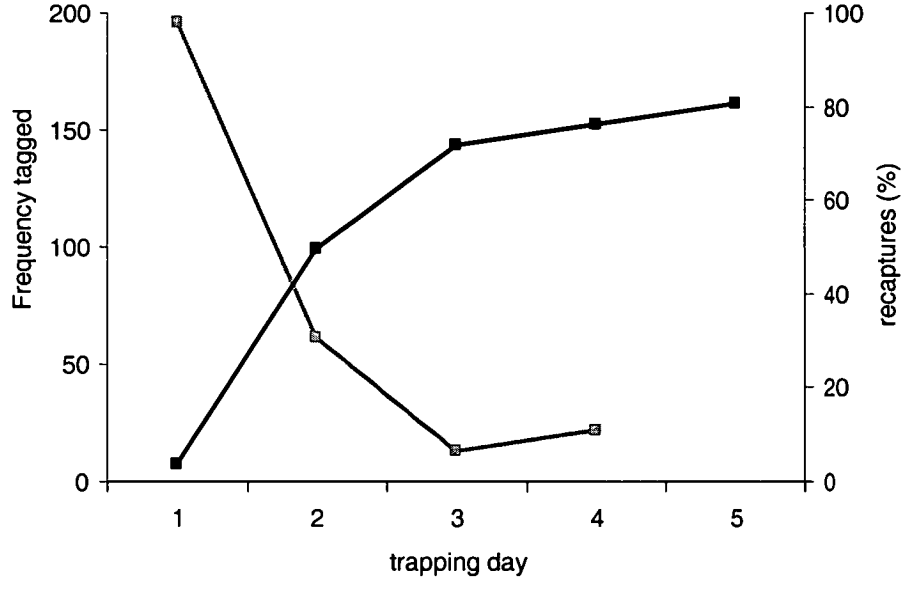

Figure 4.4: The number of *Notolabrus fucicola* tagged on four consecutive tagging days (left axis, grey symbols and line) and the proportion of tagged fish in landings by trapping day (right axis, black symbols and line).

The selectivity functions were fitted to the selectivity indices for the size classes up to and including 290 mm. The symmetrical and the asymmetrical logistic functions both described the increase in selectivity with size and yielded no significant difference on the likelihood ratio test ($\chi^2 = 0.63$, $P = 0.73$) ($\alpha = 0.05$). The symmetrical logistic function was chosen as the most parsimonious model to describe the size selectivity of the fish traps. Parameter estimates for the selectivity functions and lengths at 50% selected are presented in Table 4.1.

Table 4.1: Estimates of the parameters *a*, *b* and δ (the degree of asymmetry) for the logistic selectivity functions and l_{50} (the size at 50% selected).

Parameter	Symmetrical logistic function	Asymmetrical logistic function
a	-7.25	-6.95
b	0.039	0.038
δ	-	0.910
$l_{50\,(mm)}$	183.8	180.2

4.3.2 Inference of fishing mortality from selectivity-corrected size structure and instantaneous mortality estimates

With the exception of EHN and SC, the selectivity-corrected size structures showed a steady decline in the relative strength of size classes with increasing length. This decline starts at around 240 mm at BB, 200 mm at PB, 240 mm at TB and 230 mm at HCR and tapers smoothly to very low sample sizes in size classes above the LSL (<10% of the sample at every site, with the exception of SC) (Fig. 4.5). In contrast, the EHN site displayed consistent relative strengths of size classes until an abrupt reduction at the LSL (Fig. 4.5).

Estimates of instantaneous mortality from post-modal selectivity corrected age classes (prior to exposure to the fishery) were considerably higher than the Hoenig estimate at every site and showed no sign of inflexion at t_{LSL}, with the exception of EHN and SC which were characterised by low mortality prior to, and high mortality after, entry to the fishery (Table 4.2) (Figs. 4.6).

Table 4.2: Post modal instantaneous mortality estimates in age classes prior to exposure to the fishery, t_{LSL} and the Hoenig estimate of natural mortality.

	BB	PB	EHN	TB	HCR	SC
t_{LSL}	8	11	12	12	14	14
Mortality$\leq t_{LSL}$	0.540	0.326	0.234	0.387	0.453	0.106
Hoenig mortality	0.323	0.246	0.220	0.232	0.232	0.220

4.3.3 Influence of size-selective fishing mortality on growth parameter estimates

The growth parameters estimated using maximum likelihood with constant coefficient of variation fell within the bootstrap confidence intervals of parameter estimates fitted assuming constant variation for the L_{10} parameter at every site (Table 4.3). Inspection of the residuals plots between parameter estimation methods for each site showed no observable differences.

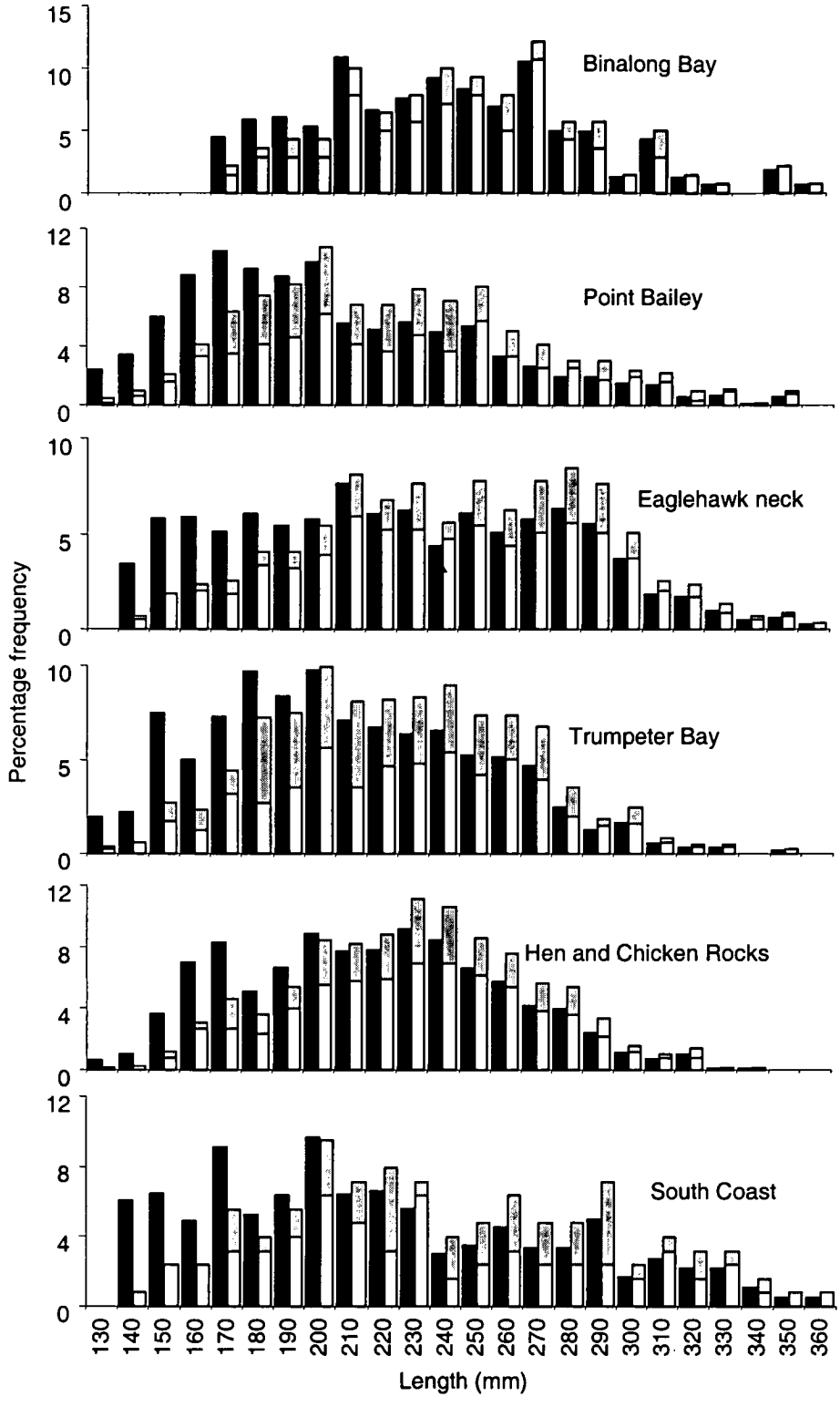

Figure 4.5: Size compositions by site. White bars are female size classes and grey are male size classes. Black bars are selectivity-corrected size classes.

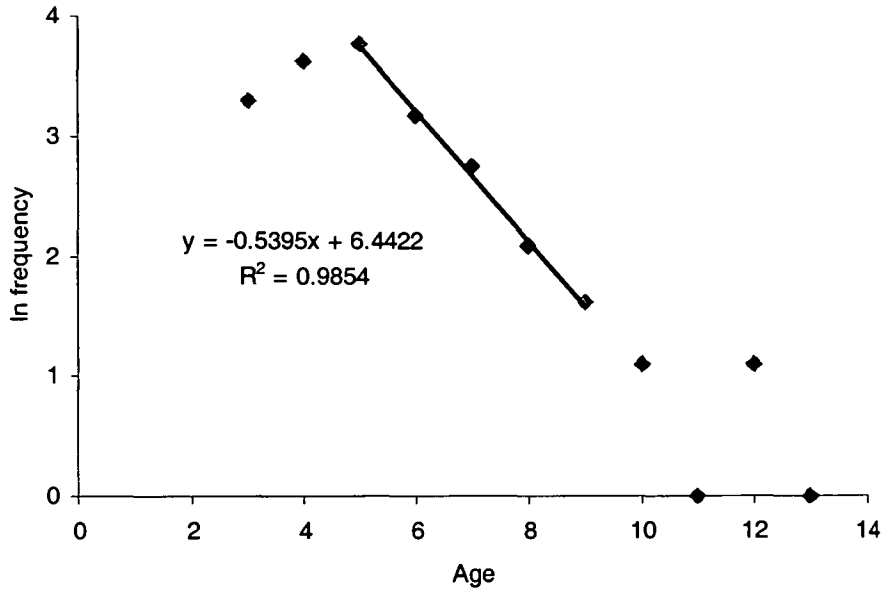

Figure 4.6 a): Catch curve for selectivity corrected age structure from Binalong Bay showing the spontaneous mortality function (black line and equation) fitted to post modal age classes prior to vulnerability to the fishery (black symbols).

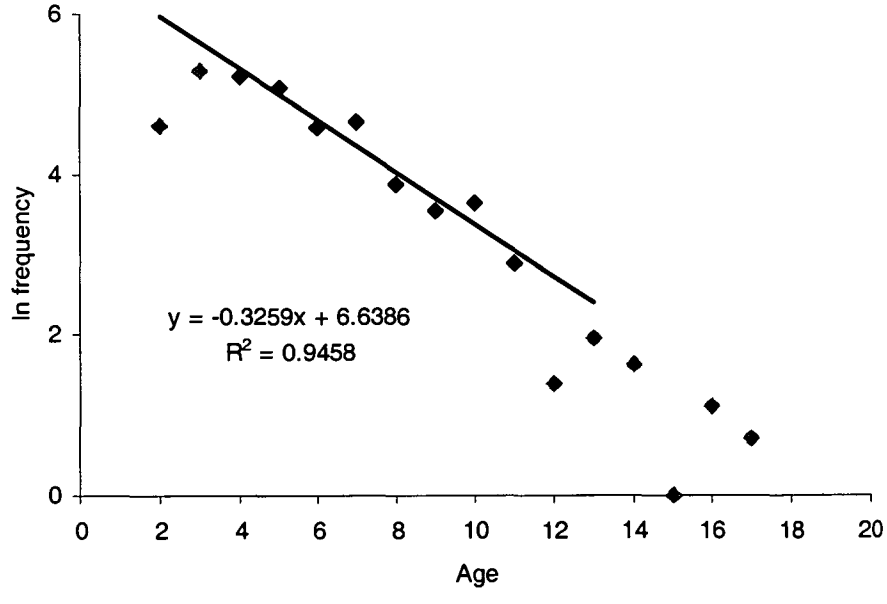

Figure 4.6 b): Catch curve for selectivity corrected age structure from Point Bailey showing the spontaneous mortality function (black line and equation) fitted to post modal age classes prior to vulnerability to the fishery (black symbols).

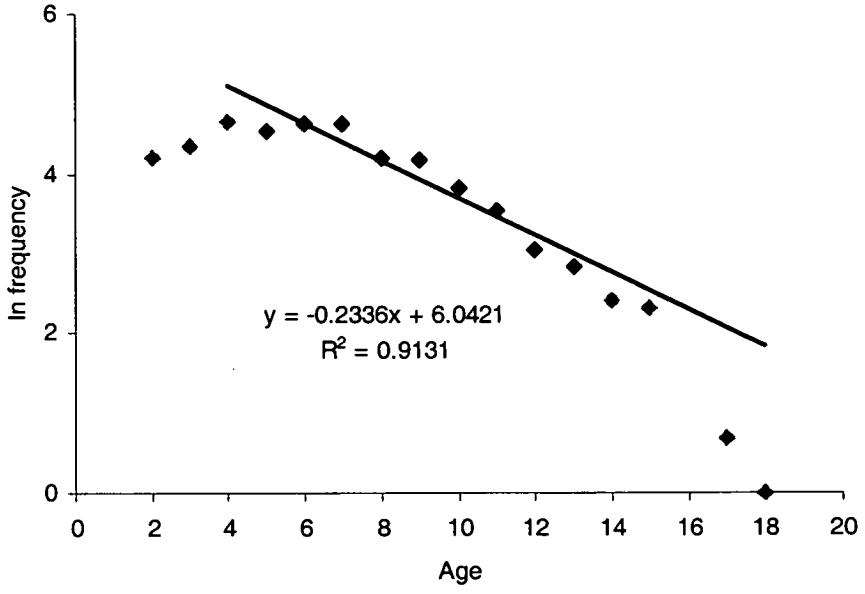

Figure 4.6 c): Catch curve for selectivity corrected age structure from Eaglehawk Neck showing the spontaneous mortality function (black line and equation) fitted to post modal age classes prior to vulnerability to the fishery (black symbols).

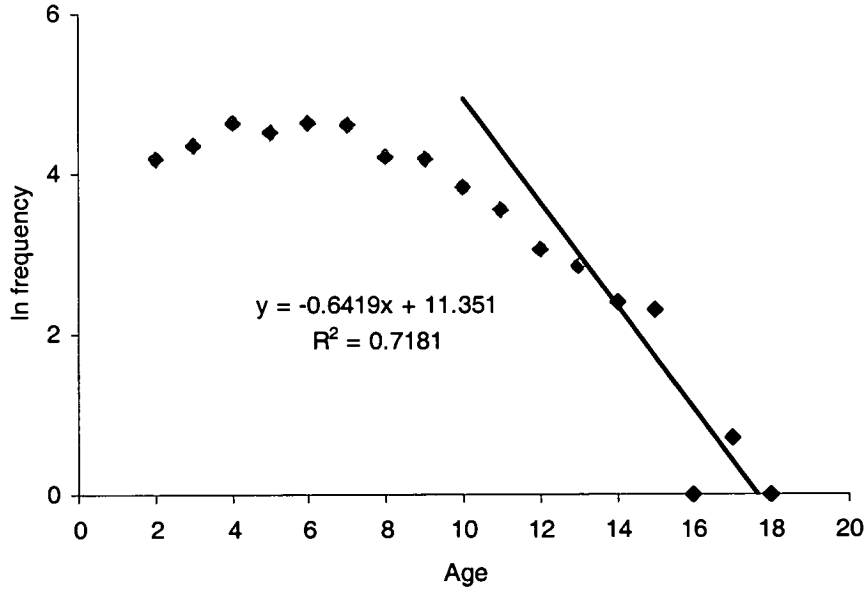

Figure 4.6 d): Catch curve for selectivity corrected age structure from Eaglehawk Neck showing the spontaneous mortality function (black line and equation) fitted to age classes vulnerable to the fishery (black symbols).

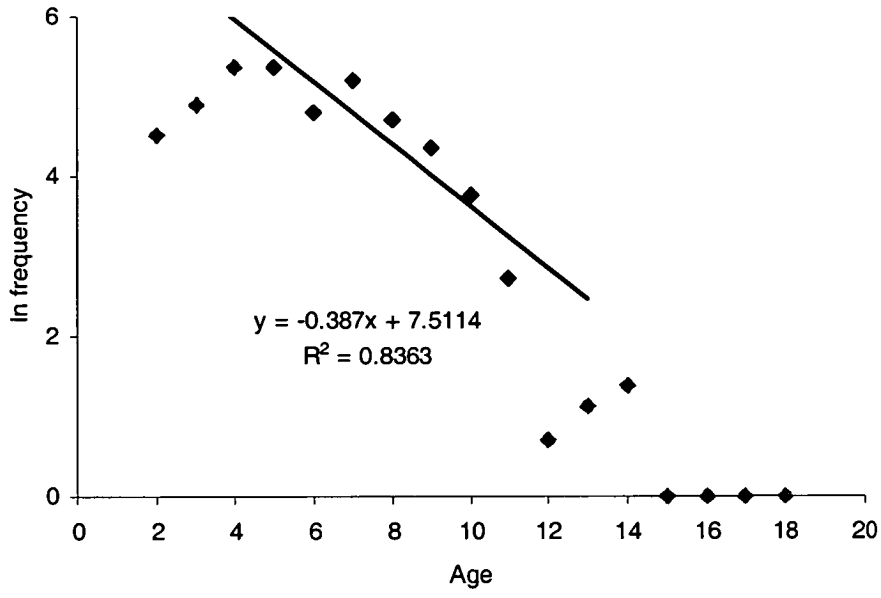

Figure 4.6 e): Catch curve for selectivity corrected age structure from Trumpeter Bay showing the spontaneous mortality function (black line and equation) fitted to post modal age classes prior to vulnerability to the fishery (black symbols).

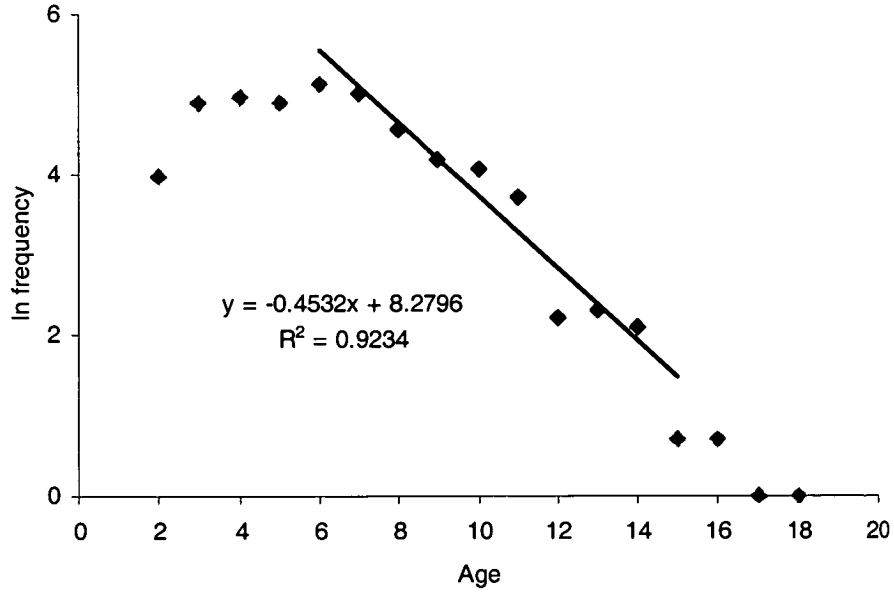

Figure 4.6 f): Catch curve for selectivity corrected age structure from Hen and Chicken Rocks showing the spontaneous mortality function (black line and equation) fitted to post modal age classes prior to vulnerability to the fishery (black symbols).

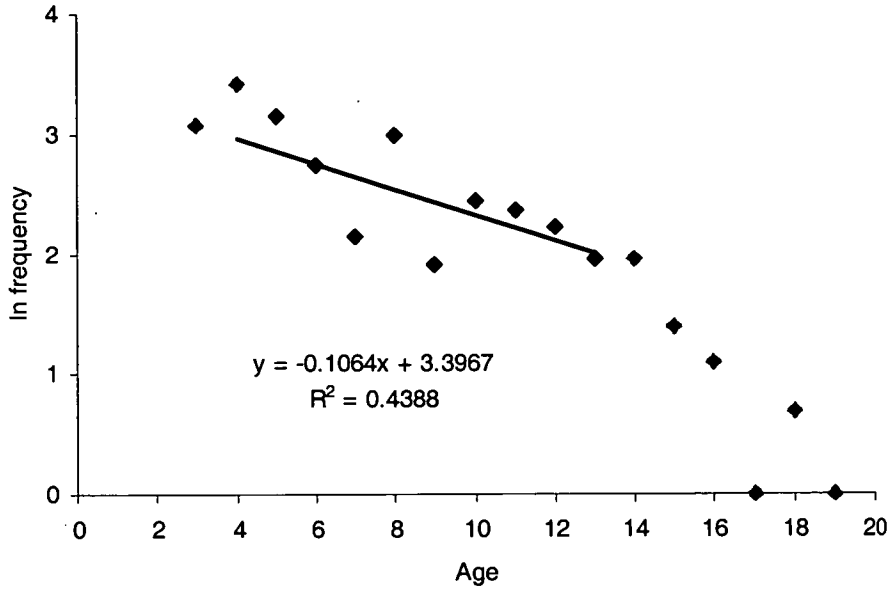

Figure 4.6 g): Catch curve for selectivity corrected age structure from South Coast showing the spontaneous mortality function (black line and equation) fitted to post modal age classes prior to vulnerability to the fishery (black symbols).

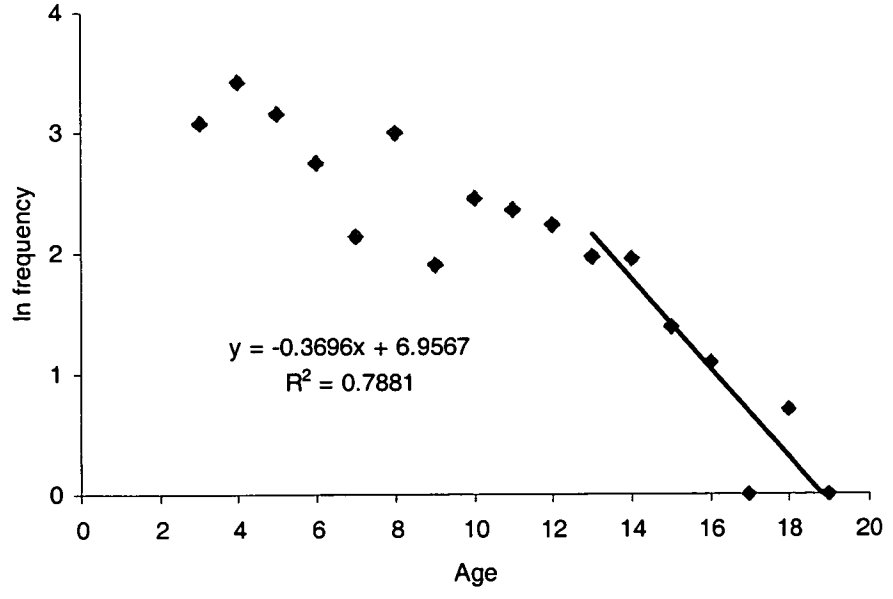

Figure 4.6 h): Catch curve for selectivity corrected age structure from South Coast showing the spontaneous mortality function (black line and equation) fitted to age classes vulnerable to the fishery (black symbols).

Table 4.3: Estimates of the parameter L_{10} (mean age at 10 years) of the reparameterised VBGF by site. Parameters were estimated using least squares methods assuming constant variation of residuals (CV) and maximum likelihood methods assuming constant coefficient of variation (CCV). Bias-corrected bootstrap 95% percent confidence intervals presented were fitted using least squares methods assuming constant variation.

Parameter	BB	PBm	PBf	EHN	TB	HCR	SC
L_{10CV}	323.5	275.0	287.8	281.5	279.4	270.3	259.1
L_{10CCV}	323.0	274.2	287.2	281.4	278.4	269.7	259.0
L_{10}lower	314.20	271.8	284.8	279.7	276.2	268.5	254.0
L_{10}upper	330.3	278.7	291.1	283.3	280.9	272.1	264.8

4.3.4 Selectivity by sex

Females dominated samples collected during the spawning season at every site and the chi-squared tests yielded significant departure from unity in sex ratios at every site for samples collected during the spawning season (Table 4.4). Sex ratios did not depart significantly from unity for samples collected outside the spawning season, with the exception of EHN where females dominated irrespective of reproductive activity. Selectivity corrected size structures did not differ significantly by sex at any site using the Kolmogorov Smirnoff two-sample test (Table 4.5).

Table 4.4: Results from Chi-squared tests for the departure from unity of sex ratios by reproductive status and within sites. Samples collected during and outside the spawning season are referred to as SP and NSP (respectively). Significance was accepted at $\alpha = 0.05$. Significant departures from unity are in bold type.

	PB		EHN		TB		HCR	
	SP	NSP	SP	NSP	SP	NSP	SP	NSP
n_{female}	316	74	320	113	313	152	363	167
n_{male}	179	63	105	54	206	145	109	143
χ^2	37.9	0.88	108	20.8	22.1	0.16	137	1.86
$P_{0.05}$	**<0.001**	0.35	**<0.001**	**<0.001**	**<0.001**	0.68	**<0.001**	0.17

Table 4.5: Results from pair-wise comparisons of selectivity adjusted size compositions by sex, within sites, using Kolmogorov Smirnoff two-sample tests. Significance was accepted at $\alpha = 0.05$. No significant differences were detected.

	BB	PB	EHN	TB	HCR	SC
n_{female}	107	390	433	465	530	77
n_{male}	34	242	159	351	252	49
D_{crit}	0.267	0.111	0.126	0.096	0.104	0.248
D	0.070	0.101	0.102	0.091	0.033	0.189

4.4 Discussion

The simulated fishdown of *Notolabrus fucicola* generated a population of tagged fish of known size structure that included strong sample sizes in size classes across the range of selectivity of the traps (Fig. 4.3). The plateau in the proportion of tagged fish in recaptures on the 4th and 5th fishing days (Fig. 4.4) suggested that the tagged population was also representative of the resident population of the reef within the size range vulnerable to capture with traps. Fishing of the tagged population allowed direct estimates of selectivity indices for a range of size classes, which were

subsequently modelled using a logistic function to generate a selectivity function for the traps.

The selectivity of a baited trap is determined by size related probabilities of fish encountering, entering and escaping prior to retrieval. It is unlikely that the probability of *N. fucicola* encountering a trap was strongly size related because (for the size classes sampled) they are a site-attached species whose home range is not size related and exceeds the size of the reef sampled (Barrett, 1995a) (Fig. 4.1). It is plausible that whilst the home range of smaller fish encompasses the entire reef, slower swimming speeds and the short trap soak times may have reduced their probability of encountering the gear relative to larger faster swimming fish. However this effect was likely to be minimal due to the small size of the reef sampled and the use of six traps set concurrently.

The dimensions of the trap entrance are unlikely to have influenced size related probability of entry, as the girth of largest fish caught was still narrower than the entrance width. Size-related density-dependant factors (Miller, 1990, Gobert, 1998) are unlikely to have influenced the probability of trap entry due to the short soak times (and consequently low catch rates) and the constant presence of bait. Entry of small individuals is likely to have been influenced by predator avoidance resulting in a reticence to leave the protection of the algal canopy (Finstad *et al.*, 2000).

Factors affecting the escape of fish from traps include bait depletion (Miller, 1990, Gobert, 1998), fish size in relation to trap mesh or escape gap dimensions (Stewart and Ferrell, 2003), and density-dependant factors (saturation) (Miller, 1990, Gobert, 1998). Bait depletion and density-dependence were unlikely to influence escape in

this study due to the short soak times and constant presence of bait. The mesh size of the traps was considerably smaller than the girth of the smallest fish caught suggesting that mesh size did not influenced the size related probability of escape. Although studies have shown that fish will squeeze through meshes considerably smaller than their size (Gobert, 1998), and that fish have bent the wire mesh of traps in order to escape (Sutherland *et al.*, 1991), the knife-edged selection likely from such a physical mechanism of escape (Stewart and Ferrell, 2003) is not present in the data.

Although the funnel shape of the trap entrance is designed to deter escape, *N. fucicola* were observed leaving the traps through the entrance with relative ease. This behaviour has been shown to be related to the direction of the current through the trap entrance (upstream is easiest) (Whitelaw *et al.*, 1991), however, due to low tidal range (<1m) and a high level of exposure at the sample site, the predominant water flows experienced were a constant fluctuation from ocean swells. Smaller fish are likely to escape through the entrance with more ease as they have more clearance (although the larger fish still had around 10 mm clearance and were observed escaping through the entrance with similar ease). Thus, it appears that the low selectivity for smaller fish and its increase in proportion with size is explained more by behavioural factors (such as reticence to leave the algal canopy) than by issues of mesh size.

This reasoning, however, does not explain the dramatic fall in selectivity at around 300 mm FL (the minimum legal size in the commercial wrasse fishery). Despite a girth that should not have interfered with trap entry, very low numbers of fish above 300 mm FL were tagged and/or recaptured. Low sample numbers in a size category have been reported to produce ambiguous selectivity indices (Hovgard *et al.*, 1999). The low selectivity above 300mm FL is unlikely to reflect a trend in trap selectivity,

but is more likely to indicate unstable selectivity indices that are the result of low sample numbers due to fishing mortality. The extensive and successful use of traps with identical entry dimensions in the fishery to target legal size *N. fucicola* (Lyle and Hodgson, 2001) supports this hypothesis.

Whilst a non-decreasing monotone function such as the logistic curve would normally be used to model selectivity for traps (Hovgard *et al.*, 1999, Millar and Fryer, 1999), the narrow entrance of the traps used in this study (Fig 4.2) had the potential to restrict entry of large fish and warrant consideration of a unimodal function. However, the plausible explanation for the low sample sizes beyond the peak selectivity index and the considerable clearance between the width of the sample entrance and the girth of the largest fish encountered, support the suggestion that any downward trend in selectivity with size had not been reached. Consequently, selectivity indices were fitted to a logistic function and indices for size classes above the minimum size limit of the fishery, were excluded from the model. Both the symmetrical and the asymmetrical logistic functions described the relationship between size and selectivity adequately and similarly (Table 4.1) (highly non-significant difference). Given the robust sample sizes of smaller fish, the selectivity curve generated would be useful for correcting size-selective sampling bias in size classes from (150 mm FL).

Indirect methods of deriving the selectivity of the fishing gears that require the deployment of multiple gears, have been shown to yield biased age structure and may violate assumptions of constant effort (Finstad *et al.*, 2000, Jensen and Hesthagen, 1996). Direct methods (such as mark recovery) have been used successfully in small lakes, but require a large number of marked and recaptured fish in open marine

systems to adequately represent the sampled population (Millar, 2000, Anganuzzi *et al.*, 1994), although recent developments have seen multiple tagging experiments combined to provide sufficient data (Myers and Hoenig, 1997). Deriving selectivity directly using mark recovery methods in this study required considerably fewer fish to mark a representative proportion of the population, due to the life-history of the species (*N. fucicola* are site attached) and the isolation of the reef sampled.

Selectivity-corrected size structure and mortality estimates implied that fishing mortality was influencing populations both above and below the LSL. However, manipulations of the error structure of growth parameter estimates suggested that this effect was not biasing growth modelling.

The trend at most sites of steadily decreasing abundance from sizes well below the LSL (Fig. 4.5) could be interpreted as high natural mortality. However, the EHN and SC sites displayed relatively stable size classes until the LSL where abundance at EHN fell abruptly (Fig. 4.5). This, combined with much lower estimates of instantaneous mortality at EHN and SC (Table 4.2), suggest that fishing mortality has depleted the populations at BB, PB, TB and HCR prior to the LSL.

The Tasmanian live wrasse fishery targets *N. fucicola* above the LSL and is unlikely to cause substantial mortality in size classes below the LSL because fishing methods (traps and barbless hooks) and handling procedures are designed to minimise mortality for live export. However, the areas of inshore reef sampled in this study are subjected to considerable fishing effort from commercial and recreational gill mesh nets (Lyle and Hodgson, 2001). Mesh sizes vary from 140 mm (stretched mesh), which is routinely deployed to target *Cheilodactylus spectabilis* down to 100 mm

(stretched mesh), which is used extensively by the commercial and recreational sector to target *Seriolella brama* and *Latridopsis forsteri* (Lyle and Hodgson, 2001). *Notolabrus fucicola* are particularly vulnerable to the smaller mesh gillnets and typically suffer poor survival due to barotrauma and excessive scale loss (personal observation). The EHN site is situated adjacent to a small marine reserve where gillnetting is banned and, whilst the site is not within the reserve, confusion within the fishing fraternity over its borders may have lead to a reduction in small mesh effort in the area. The abrupt increase in mortality at the LSL at EHN is consistent with fishing mortality from the live wrasse fishery that uses fishing methods that are permitted in the reserve (trapping and hooks).

The SC site is situated on a highly exposed coastline and is beyond the range of the aluminium outboard powered dinghies typical of the live wrasse and gillnet fisheries. Thus, a plausible hypothesis for the trends in size structures and instantaneous mortalities, attributes the high mortality beginning below the LSL at BB, PB, TB and HCR to fishing mortality (i.e. undersized by-catch in the small-mesh gillnet fisheries), attributes lower mortality at EHN to reduced gillnet effort, attributes the knife-edge onset of fishing at the LSL at EHN to commercial wrasse fishing and suggests SC is subjected to little fishing effort and that its instantaneous mortality estimate is more likely to reflect natural mortality at that site.

Given that the degree to which growth parameters are affected by size selective fishing mortality is dependent on the rate of the onset of fishing activity, the most likely site to be affected is EHN where the onset of fishing mortality appears to be knife-edged at the LSL. If the selective removal of faster growing fish is sufficiently strong, it would result in an overestimation of the predicted age at the LSL (Sinclair *et*

al., 2002a), a lower estimate of L_{10} (the parameter of mean size at 10 years) and the parameter estimation procedure assuming constant coefficient of variation (reducing the 'leverage' exerted by high values with a high residual term) would be expected to yield higher values of L_{10}. However, estimates of the parameter L_{10} derived from parameter estimation assuming constant coefficient of variation, fell within the bootstrap confidence intervals of the parameter estimates derived under assumptions of constant variation for every site (Table 4.3). In addition, qualitative examination of the pattern of the residuals for every site revealed no obvious differences between the two methods of parameter estimation. This result implies that either fishing mortality was not high enough (or enough focussed at the size limit) or that variation of length-at-age was not large enough, to bias parameter estimations. Alternatively, strong sample sizes at smaller lengths may have been the dominant influence on parameter estimation, irrespective of the degree of size selective fishing mortality bias.

Although females dominated catches during the spawning season, sex ratios returned to unity when *N. fucicola* were not reproductively active, with the exception of EHN where females remained dominant in catches throughout the year. Reduced catch rates of male *N. fucicola* during the spawning season are consistent with observations that they devote less time to foraging activity whilst reproductively active (Barrett, 1995b, Denny and Schiel, 2001). Despite the dramatic differences in sex ratio by reproductive status, the size structures by sex were not significantly different at any site. This implies that whilst reproductive status structures sex ratios in samples, it is not necessary to incorporate it into the size-selectivity model because the relative proportions of the size classes (and hence age classes) are unaffected by reproductive

status at the time of sampling. This also permits the size selectivity function to be fitted to both sexes for reconstructed size and age structures.

Size-selective biases in a dataset must be considered when making inferences about the sampled population (Frusher and Hoenig, 2001). This is particularly important when parameters are sensitive to size-selective biases (such as age structure) and are compared between populations. The fish traps used in this study displayed considerable size selectivity which necessitated the use of the selectivity function to both indicate size/age classes that can be compared robustly and correct size and age structures to allow robust comparison of size/age classes.

Fishing mortality has the potential to bias relative year class strengths and confound comparisons of age composition and growth rates between populations (particularly with varying or unknown levels of exploitation). The sites sampled in this study displayed varying fishing profiles and levels of exploitation, necessitating consideration of size-selective fishing mortality when interpreting relative year class strengths within site and comparing age compositions between sites. The knife-edged onset of fishing mortality at EHN did not appear to bias growth parameter estimates, allowing the use of parameter estimation methods assuming constant variation when modelling growth.

Chapter 5: Spatial and temporal variation in the age composition of *Notolabrus fucicola*

5.1 Introduction

Age composition is a fundamental biological parameter and is crucial to understanding population structure and a fundamental requirement in fisheries management (Ferreira and Russ, 1995), as strong recruitment variations can increase the potential for over-fishing (Morison *et al.*, 1998). Age composition derived from adult age data may also provide an insight into the processes that have structured a population up to the point of sampling (Meekan *et al.*, 2001). Events in early life history, such as larval survival to settlement and post-settlement density-dependent mortality are likely to have a dramatic and enduring influence on adult age composition. This is due to the inherent risks in dispersive larval strategies, increased densities and mortality in new settlers, and generally decreasing predation with increasing size (Gust *et al.*, 2002).

The fishing gear used to sample a population will rarely target all components of the population equally (Ricker, 1975). Size-selectivity in catches reduces year class strength in poorly selected size classes and produces strong year class strengths in well selected size classes (Newman *et al.*, 1996b, Finstad *et al.*, 2000), limiting the ability to interpret signals from early life history stages. Gear selectivity has been addressed in previous research by using a range of sampling gears to generate age data, although the degree of overlap (or lack of overlap) can bias relative year class strengths (Finstad *et al.*, 2000). Despite the biases likely to be caused by gear selectivity, it has not always been considered and has rarely been quantified in studies estimating age composition.

Adult age structure can be used to interpret early life history events provided the target species is sufficiently long-lived and experiences low natural mortality in adulthood (Meekan *et al.*, 2001, Levin *et al.*, 1997). However, other sources of adult mortality such as size-selective fishing mortality may dramatically alter population structure (Edgar and Barrett, 1999), such that signals from early life history events are completely obscured through disproportionate depletion of targeted size classes (Ferreira and Russ, 1995). Clearly, age structure is a powerful tool to examine the effect of fishing mortality on a population, however, if the objective is to examine the extent of year-class variability, failure to correct for gear selectivity and to consider the impact of fishing mortality on targeted year classes could lead to erroneous conclusions. These considerations are particularly important when comparing age compositions between populations with varying or unknown levels of fishing mortality (Choat *et al.*, 2003).

The aims of this chapter were twofold. Firstly to determine the age structure of populations of *Notolabus fucicola* on the east and southeast coasts of Tasmania by correcting raw age compositions for the size-selectivity of the sampling method. Secondly, temporal and spatial trends in selectivity-corrected relative year class strengths were examined with consideration of the impacts of fishing mortality on age structure (see Chapter 4) to infer the role of early life history events in structuring adult populations.

5.2 Materials and methods

5.2.1 Sampling

Refer to 3.2.1 for sampling methods.

5.2.2 Age estimation

Refer to 3.2.2 for age estimation methods.

5.2.3 Raw age composition

A year class (birthyear) was assigned to each fish on the basis of its age estimate and an assigned birthdate of the 1st of October (See Chapter 2). The age composition of each site was based on the frequency distribution of year classes.

5.2.4 Truncation of biased year classes

Age compositions were truncated to remove the biases associated with low selectivity of small fish. As year classes were formulated from fish sampled over two years, the variation of size within a year class was a combination of the variation of size-at-age within the age classes and the growth between them. Thus year classes encompassed a considerable range of sizes, particularly at low ages when growth was fastest. To minimise the influence of low numbers of poorly selected (and hence heavily weighted) fish on relative year class strengths, year classes were excluded if the one tailed 95% confidence interval below the mean was less than 150 mm FL (see Chapter 4).

5.2.5 Selectivity correction of raw age composition

A symmetrical logistic selectivity function, derived from a simulated fish-down using tags at a reef adjacent to the Point Bailey site (see Figs. 3.1 and 4.1), was used to correct for gear selectivity bias in relative year class strengths.

$$r(l) = \frac{e^{(a+bl)}}{1+e^{(a+b(l)}}$$

where $r(l)$ is the selectivity of a fish of size l. Details of the selectivity trial and modelling of selectivity indices are provided in Chapter 4.

Three methods were used to correct the age compositions for gear selectivity bias in relative year class strengths. Method 1 involved weighting each individual fish by the inverse of the selectivity predicted by its length. Method 2 involved weighting each individual fish by the inverse of the selectivity predicted by the mean length-at-age for its age estimate. For these two methods, the frequency for each year class was the sum of the weightings. Method 3 involved dividing the frequency for each year class by the selectivity predicted by the mean length of that year class. This method is analogous to a common approach encountered in the literature where the frequency for each age class is multiplied by the selectivity predicted by the mean length-at-age for that age class. As sampling extended beyond one year in this study, year classes were not synonymous with age classes.

The age structures generated from each of the 3 methods of selectivity correction (including uncorrected) were tested pair-wise for significant differences by site using the Kolmogorov-Smirnov two-sample test (Sokal and Rohlf, 1995). The level of significance of differences between selectivity adjustment methods was adjusted for the number of dependent comparisons using the Bonferroni method.

5.2.6 Spatial comparisons of age compositions

Selectivity-corrected age compositions were compared pair-wise among sites using the Kolmogorov-Smirnov two-sample test. The level of significance of differences between sites was adjusted for the number of comparisons using the Bonferroni method.

5.3 Results

5.3.1 Raw age composition

At each site the raw relative year class strengths rose steadily from the youngest fish (born between 1997 and 1999) to a peak prior to a general decline with increasing age (Figs. 5.1). This peak was evident in 1992 at PB, EHN, TB and HCR, 1997 at BB, and 1994 at SC. At PB, TB and SC there was a distinct reduction in year class strength in 1993 relative to adjacent year classes and at EHN a reduction in relative year class strength in 1991. The oldest fish was 19 years of age (with a birthyear of 1980) sampled from EHN. The number of year classes encountered ranged from a maximum of 19 at EHN to a minimum of 11 at BB. With the exception of BB and SC (which were sampled later), age compositions were dominated by the year classes from 1989 to 1996, which comprised more than 80% of the age composition and included fish from 2 to 11 years of age at every site.

5.3.2 Truncation of biased year classes

Truncation of younger year classes (to minimise the magnification of errors inherent in large corrections of poorly selected year classes) excluded the 1997 and 1998 year classes at PB, EHN, TB and HCR, and the 1999 year class at PB, EHN, TB, HCR and SC. The age classes truncated were characterised by very low sample numbers but the truncation excluded less than 5% of the sample at every site.

5.3.3 Selectivity correction of raw age composition

The age compositions generated by the three methods of correction for the size-selectivity of the fish traps did not differ significantly at any site ($P > 0.95$ for every comparison at every site) in pair-wise comparisons using the Kolmogorov Smirnoff

two-sample test ($\alpha = 0.0083$ adjusted using the Bonferroni method for 6 dependent comparisons within site). However the uncorrected age composition differed significantly from each of the three correction methods ($P < 0.001$ for every site and method). Given that the three correction methods produced equivalent results for every site, method one was considered to be more robust because each individual was weighted on the basis of its size, giving greater weight to slower growing individuals within as well as between year classes. This approach was desirable because sampling was conducted regularly over two years, resulting in year classes that were composed of individuals from more than one age class. Consequently method 1 was used for all subsequent selectivity corrections. The correction for selectivity generally boosted the relative importance of younger year classes (Fig. 5.1). The maximum weighting applied by the selectivity correction was a factor of 2.8 for the 1996 age class at TB.

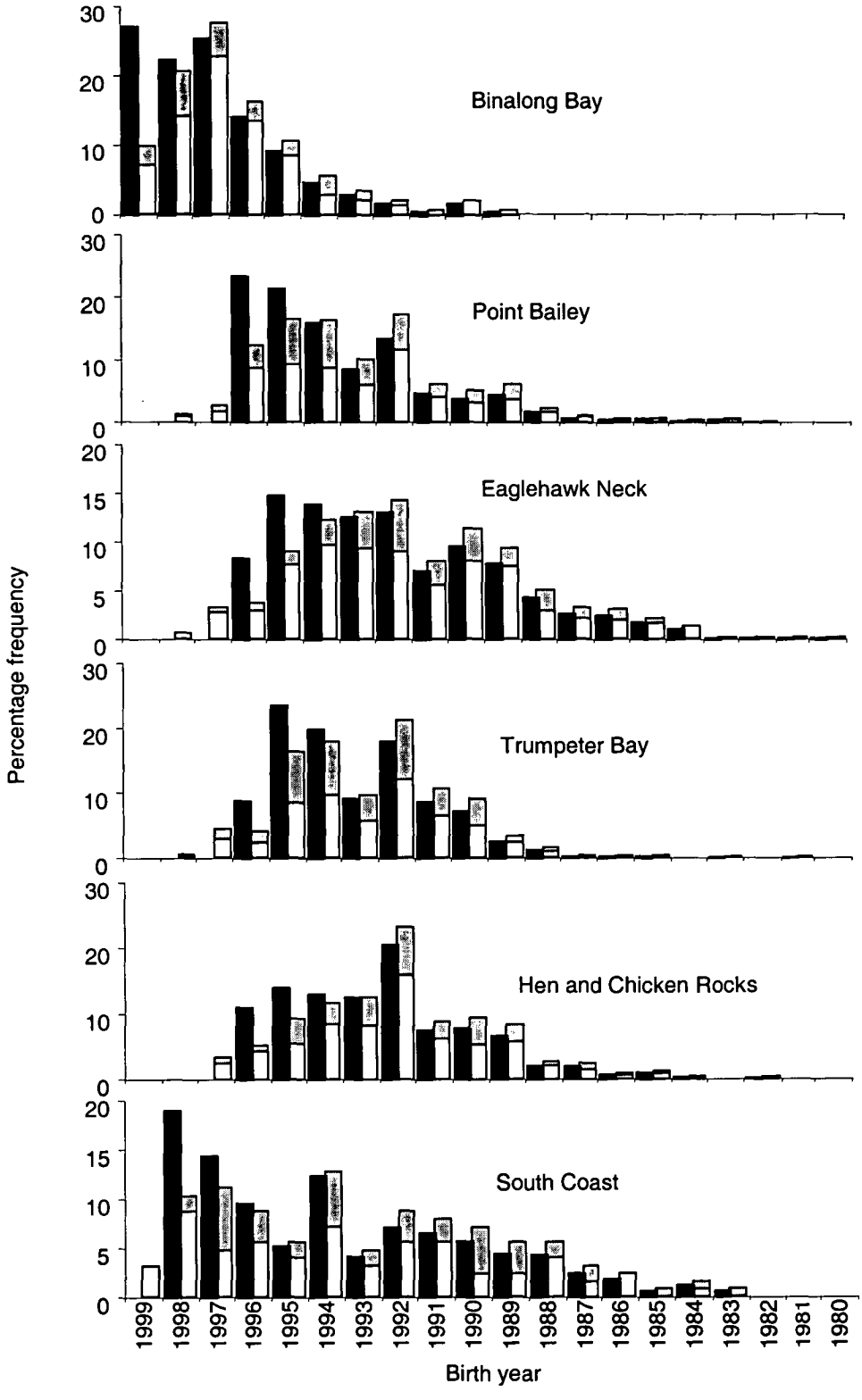

Figure 5.1: Age compositions of *Notolabrus fucicola* by site. White bars are female year classes and grey are male year classes. Black bars are year classes that have been adjusted for the selectivity of the fish traps used to collect the samples and indicate the range retained after truncation of year classes likely to be biased by low selectivity.

5.3.4 Spatial comparisons of age compositions

The comparisons of truncated and selectivity-corrected age compositions yielded significant differences between every site, with the exception of comparisons between EHN and SC (Table 5.1).

Examination of selectivity-corrected year class frequency distributions (Figs. 5.1 black bars) revealed that relative year class strengths varied both within and among sites. In general, PB, TB and HCR were characterised by a steady decline (with the exception of 1992) from the 1995 year class, to relative year class strengths of less than 2% by 1988. In contrast, EHN and SC displayed a shallower decline to year class strengths of less than 2% by 1983 at EHN and 1985 at SC. The BB site was characterised by a peak in relative year class strength at 1997, followed by a rapid fall by the 1992 year class. The TB, PB and SC sites shared a distinct fall in relative year class strength in the 1993 year class. The EHN site displayed a relatively weak year in 1991, which was shared by PB, TB and HCR (although at these sites it was consistent with a general decline). The 1992 year class was strong at every site (except BB where sample sizes in older year classes were very low), but was particularly strong at HCR (Fig. 5.1).

Table 5.1: Results from pair-wise comparisons between sites of truncated age compositions (raw and selectivity adjusted) using Kolmogorov Smirnoff two-sample tests. Significance was accepted at $\alpha = 0.0033$ (adjusted using Bonferroni method for 15 dependent comparisons by site). Significant differences are in bold type.

		BB	PB	EHN	TB	HCR
PB	n	666				
	D_{crit}	0.238				
	D	**0.236**				
EHN	n	686	1176			
	D_{crit}	0.187	0.091			
	D	**0.508**	**0.222**			
TB	n	835	1383	1345		
	D_{crit}	0.237	0.082	0.087		
	D	**0.328**	**0.102**	**0.186**		
HCR	n	815	1363	1325	1532	
	D_{crit}	0.237	0.084	0.088	0.080	
	D	**0.404**	**0.203**	**0.094**	**0.141**	
SC	n	207	702	697	871	799
	D_{crit}	0.235	0.183	0.169	0.181	0.182
	D	**0.433**	**0.238**	0.138	**0.212**	**0.185**

5.4 Discussion

Variations in selectivity-corrected relative year class strengths were modest (a factor of < 2.5) indicate that *Notolabrus fucicola* are characterised by stable relative year class strengths. The spatial variation that was detected, displayed some consistency in the pattern of year classes, with a weak year in 1993 and a strong year in 1992 across most sites.

The raw age compositions displayed a steep increase in year class strength consistent with increasing selectivity to the traps. The finding that EHN yielded the earliest born

individual (1980) and the greatest range in year classes (1998 to 1980) supports the contention that EHN was subject to less fishing mortality than other sites (with the exception of SC, where smaller sample sizes could have limited the range of ages).

The selectivity function provided a clear indication of the year classes that were sufficiently selected to provide robust temporal and spatial comparisons. It also provided the ability to correct for reduced selectivity, which increased the number of year-classes that could be compared. However, interpretation of the more heavily weighted year classes should be viewed with caution, as selectivity curves are unreliable at low values of selectivity (Hovgard *et al.*, 1999). Although the truncation of poorly selected year classes (on the basis of size) was intended to address this problem, the low relative year class strength in the 1996 year class at EHN, TB and HCR may be an artefact of low selectivity rather than poor year class-strength. This could arise due to localised factors influencing the selectivity of the traps and implies that pre-modal year class strengths should still be interpreted with caution.

The sites that were subject to strong fishing mortality below the legal size limit (LSL) (i.e. BB, PB, TB and HCR) (see Chapter 4), displayed a steady fall in year class strength from the modal year class (with the exception of a strong year in 1992), to very low strength at a year class equivalent to around 11 years of age. However, the 1992 year class at PB, TB and HCR equates to mean fork lengths of 241 mm at HCR, 246 mm at TB and 248 mm at PB which are consistent with the onset of the steep decline in size structure attributed to fishing mortality (see Chapter 4). This implies that the weak year class in 1993 is unlikely to be an artefact of fishing mortality and is a product of underlying processes structuring relative year class strengths.

In contrast, the lesser fished sites (EHN and SC) displayed strong relative year classes over a broader range, reaching very low strength at year classes equivalent to approximately 16 years of age. The SC site displayed the most variation in year class strength with weak years in 1995 and 1993, with a strong year in 1994, although this structure may have been due to lower sample sizes. The broader range of ages at EHN and SC supports the hypothesis that fishing mortality is responsible for much of the structure of populations at the more heavily fished sites.

The statistical comparisons of selectivity-corrected age composition among sites yielded significant differences between every site with the exception of EHN and SC. The primary similarity between EHN and SC lies in the stronger year class strengths at greater age due to reduced early fishing mortality. Thus, the spatial variation detected in age compositions at heavily fished sites, reflects spatial variation in fishing mortality rather than underlying differences in population structure. This conclusion would warn against drawing inferences from age compositions about processes that structure those populations other than fishing mortality at the fished sites. However, the trough in 1993 and the peak in 1992, at three of the four strongly fished sites, are situated prior to the onset of early fishing mortality implying that these year classes can be interpreted with reference to processes prior to fishing mortality. The concurrence of a poor year class in 1993 at the relatively unfished SC site lends credence to the validity of the poor year class in 1993 at the fished sites. However, the lack of a relatively strong signal in 1992 at SC suggests that the peak in 1992 may only be relative to a subsequent rapid fall in year class strength at the fished sites, although HCR is dominated by the 1992 year class.

Clearly, fishing mortality interferes with the interpretation of age composition with respect to more fundamental processes. However, the advantage of two relatively unfished populations and a window in the age structure of the exploited populations, of robust year classes that are well selected yet relatively unfished, provides the opportunity to examine both the spatial and temporal variability in *N. fucicola* age composition without the impact of fishing mortality and the contribution of processes other than fishing mortality. Observations based on the window of year classes prior to substantial fishing mortality yet well selected by the fishing gear revealed fluctuations of around a factor of 2.5 between the strongest and weakest year classes.

In the absence of fishing mortality, the age compositions of adult populations of sedentary reef fish are more likely to be structured by processes in their early life history (Rickman *et al.*, 2000) due to variable mortalities in the larval stage, high densities and mortality in juvenile settlers (Tupper and Boutilier, 1995), and dramatic reductions in mortality with increasing size (Gust *et al.*, 2002). Exceptions to this premise include species with short life-spans or with episodic adult mortality. For example, the temperate labrid *Tautogolabrus adspersus* experiences high mortality during storm events whilst over-wintering (Levin *et al.*, 1997), and a territorial reef species has displayed higher mortality at the onset of maturity (Steele, 1997). However, given that *Notolabrus fucicola* are strongly site attached (Barrett, 1995b), (eliminating the dilution of signals from early-life history caused by migration and emigration), are not territorial (Barrett, 1995a) and are long-lived (see Chapter 3), fluctuations detected in adult age structure are more likely to be the outcome of events in their early life history.

The processes in the early life history that structure populations are functionally divided into pre-settlement processes (larval survival and settlement success) and post-settlement processes (post-settlement mortality). Post-settlement juvenile mortality has been found to structure populations due to density-dependent factors such as food availability, shortage of habitat (Tupper and Boutilier, 1995, Nitschke *et al.*, 2002, Jones, 1984a) and ultimately increased predation (Steele, 1997). Growth is strongly influenced by density-dependence through mechanisms such as food-limitation (Tupper and Boutilier, 1995, Rijnsdorp and Leeuwen, 1992, Sinclair *et al.*, 2002a, Marshall and Frank, 1999, Gust *et al.*, 2002, Peterman and Bradford, 1987). Populations of other temperate wrasses have been found to be structured by post-settlement processes through density-dependent growth suppression (Tupper and Boutilier, 1995, Jones, 1984b, Levin *et al.*, 1997). However, Barrett (1999) concluded that populations of the site-attached temperate wrasse *Notolabrus fucicola*, on the southeast coast of Tasmania, were not resource-limited because growth rates were similar among sites with similar habitats. This hypothesis was supported by the conclusion that growth varied spatially with an environmental gradient, and did not vary with factors likely to influence population densities such as fishing mortality or reef characteristics (see Chapters 3 and 4). This implies that post-settlement processes are not an important factor in structuring adult populations of *N. fucicola* and suggests that fluctuations in relative year class strength are more likely to be a product of variable patterns of larval settlement.

Inter-annual trends in pre-settlement processes (i.e. larval survival to settlement) have also been strongly linked to relative year class strengths in species with dispersive larval stages. The processes that influence settler numbers include egg production (Rickman *et al.*, 2000, Livingston, 2000), larval food availability (particularly when

the yolk sac is expended) (Bradford, 1992, Jones, 1984b), temperature (Morehead and Hart, 2003), transport processes (Livingston, 2000) and predation (Jones, 1984b). Densities of larval settlers have been linked to coastal processes such as hydrology and climate (eg. El Niño-Southern Oscillation Events) (Meekan *et al.*, 2001), and primary productivity (Thresher *et al.*, 1989, Harris *et al.*, 1988), with variations in these factors shown to produce highly fluctuating year class strengths (Livingston, 2000, Harris *et al.*, 1988, Bruce *et al.*, 2001, Ralston and Howard, 1995, Jordan, 2001a). The east and southeast coasts of Tasmania are characterised by a high degree of temporal and spatial variability in hydrographic and climatic conditions (Harris *et al.*, 1988). Primary productivity on these coasts, during the spawning season of *N. fucicola* is highly variable in time and space and is driven by the relative position of the nutrient-poor east Australian current and nutrient-rich water of sub-Antarctic origin. The position of these dominant water masses on the shelf and levels of phytoplankton and zooplankton production are also influenced by the degree of westerly wind stress (Harris *et al.*, 1988, Young *et al.*, 1993). These conditions have a dramatic effect on the survival of pelagic larvae to settlement through food availability and transport (Bruce *et al.*, 2001, Thresher *et al.*, 1989), and have resulted in highly variable year class strengths in other local species (Jordan, 2001a, Bruce *et al.*, 2000). Given that *N. fucicola* are pelagic in their larval stage (Welsford, 2003a), and hydrology of the Tasmanian coast is variable at scales likely to affect larvae, it would be expected that the density of settlers would vary in space and time.

Notolabrus fucicola have an extended spawning season from August to January (Barrett, 1995a) and it would appear that the long spawning season maximises the likelihood that some proportion of their larvae will encounter favourable feeding conditions given the high intra-annual variability of coastal productivity. This

strategy would be likely to yield the modest variation in relative year class strengths observed in *N. fucicola* in this study, and support the hypothesis that post-settlement mortality does not strongly influence the structure of adult age composition.

In conclusion, the age composition of *N. fucicola* is characterised by generally low variability in relative year class strengths. Due to an apparent absence of density-dependent growth, the detected fluctuations are likely to reflect variations in the density of larval settlers. The modest degree of variation is consistent with the hypothesis that the long spawning season *N. fucicola* results in only modest variations in larval settlement. This study also shows that if the selectivity of the sampling gear and the influence of fishing mortality were not considered in the interpretation of year class strengths, conclusions about the influences structuring populations could be profoundly erroneous.

Chapter 6: General Discussion

The processes that determine size and age composition are functionally divided into those that are pre-settlement (governing egg and larval survival to settlement) and those that are post-settlement (governing growth and survival after settlement). Determining adult age composition and growth patterns can provide a means of examining the significance of these processes in determining population structure (Meekan *et al.*, 2001), and as the factors that influence such events vary in time and space, spatial and temporal comparisons of age composition and growth are particularly informative. Spatial comparisons of adult age composition and growth of *Notolabrus fucicola* were utilised as a means of examining whether resource-limitation was evident in discrete populations over large spatial scales. *Notolabrus fucicola* were well suited for inferring the relative importance of such processes from adult age and growth data, due to their longevity (19 years maximum age detected in this study), low adult natural mortality (Barrett, 1995a) and site attachment (Barrett, 1995a).

To ensure that the estimation of age composition from samples represented the population, the accuracy of age estimates, size-selectivity biases and sources of strong adult mortality were examined. Firstly, the ageing methodology involved a comprehensive validation, consistent with processes detailed in Campana (2001). Biases in the size and age structures caused by the size-selectivity of the sampling gear were then estimated to ensure the samples best reflected the sampled populations. Finally, spatially variable fishing mortality was estimated and considered when interpreting age structure. These aspects of this study allowed robust

spatial comparisons of growth rates and age compositions, and improved the ability to infer the processes structuring populations of *N. fucicola* in Tasmanian waters.

Although growth is strongly influenced by density-dependence (Jones, 1984b, Tupper and Boutilier, 1995), growth rates did not vary spatially with factors likely to affect the ratio of stock density to resources (such as habitat structure, fishing mortality, local hydrography or diet items), and was best explained by the spatial trend in water temperature. The positive relationship between growth and water temperature supports the hypothesis that *N. fucicola* do not achieve sufficient post-settlement abundance to suffer density-dependent growth variations. This finding is consistent with Barrett (1999) who suggested that resource-limitation was not evident in populations of *N. fucicola* on the east coast of Tasmania.

This conclusion is dependent on the degree to which growth rates and size-at-age in adult fish reflect density-dependent conditions in juvenile stages and is a function of the persistence of patterns of size-at-age from early life into size-at-age of adults. Dramatic interannual variation in the growth of individuals would mask the effects of post-settlement density-dependent growth suppression. *Notolabrus fucicola* may experience interannual variation in growth from factors such as interannual fluctuations in reef productivity and/or densities of interspecific competitors. Although, this effect would be exacerbated by density-dependent conditions in adulthood, such conditions are unlikely on the east and southeast coasts of Tasmania due to considerable fishing mortalities of *N. fucicola* and other generalist predators cohabiting inshore reefs (such as *Notolabrus tetricus* and *Cheilodactylus spectabilis*) (Welsford, 2003a, Lyle and Hodgson, 2001, McCormick, 1998). Further study is advocated to examine interannual variability in growth using methods to generate

individual growth trajectories such as tag recapture studies or back-calculation, to assess the degree to which growth in early life is reflected in adult size-at-age.

The age composition of *N. fucicola* was characterised by generally low temporal variability in relative year class strengths. Whilst some variation in the pattern of unfished year classes was evident among sites, the factor that produced the most obvious spatial differences was exposure to fishing mortality below the legal size limit (LSL). This result underscores the ability of fishing mortality to dramatically alter population structure (Choat *et al.*, 2003). Given that density-dependent processes are unlikely to structure adult populations of *N. fucicola*, the low variation in year class strengths is likely to reflect low variation in the numbers of larvae settlers.

The age structure of *N. fucicola* populations supports the hypothesis that the low recruitment variability in the temperate reef species that reside on the Tasmanian east and southeast coasts reflects their reproductive and larval strategies. *Notolabrus fucicola* have an extended spawning season from August to January (Barrett, 1995a). Their eggs hatch after 2-5 days and the larvae have a highly plastic growth rate and pelagic larval duration (settling on inshore reefs after 30 to 70 days) (Welsford, 2003a). These strategies are consistent with other temperate inshore species, such as *Platycephalus bassensis* who also have a protracted spawning season of up to 6 months and a similar larval duration (up to 3 months) (Jordan, 2001b) and are also characterised by low recruitment variability (less than a factor of 2) (Jordan, 1998). In contrast, the temperate scalefish *Nemadactylus macropterus* and *Latris lineata* have extended larval durations of around 10 months and shorter spawning seasons, and are characterised by considerable fluctuations in year class strengths (of an order

of magnitude) (Jordan, 2001c, Murphy and Lyle, 1999). It would appear that the shorter inshore larval duration, in combination with an extended spawning season, maximises the likelihood that some proportion of their larvae will encounter favourable feeding conditions and settlement habitats. Moreover, the variable pelagic larval duration and larval growth rate of *N. fucicola* may maximise their chance of surviving until settlement size is reached. This supports the hypothesis that pre-settlement processes are likely to be an important mechanism in determining *N. fucicola* age composition.

Whilst post-settlement mortality is unlikely to be a dominant influence on adult age structure, a more pluralistic approach to the relative roles of pre and post-recruitment processes is advisable. Irrespective of the degree of fluctuation in settler densities, every year class would be expected to experience density-dependent mortality (Steele, 1997), and detection would rely on the spatial scale of the investigation (Sale, 1976, Levin *et al.*, 1997, Steele, 1997). For example, recruitment has been found to be more episodic and hence exert more influence over population structure at the edge of the distribution of a species (Levin *et al.*, 1997). Furthermore, density-dependent mortality would be expected to be highest in strong year classes and would generally ameliorate the expression of fluctuations of settler densities in adult age structure (Ralston and Howard, 1995, Doherty and Fowler, 1994, Jones, 1991). Thus, the low variation in relative year class strength may indicate that strong post-settlement mortality is levelling strong year classes to the carrying capacity of individual reefs. This hypothesis seems unlikely in *N. fucicola* because site differences in hydrology (and hence larval supply) and spatial differences in the distribution of reef habitat (Barrett *et al.*, 2001) did not result in high spatial variation in age compositions. A more plausible alternative hypothesis is that pre-settlement processes govern settler

densities, after which density dependent juvenile mortality is only experienced by very strong year classes (Jones, 1984b).

The spatial gradient of growth rates detected in *N. fucicola* has implications for management of the wrasse fishery. The current management strategy of a State-wide legal size limit (LSL) (300 mm) results in *N. fucicola* becoming vulnerable to the fishery at 13 years of age on the south coast and only 8 years on the north east coast of Tasmania. A difference of this magnitude implies a substantial difference in the amount of protection provided by the LSL to spawning stock between these spatial fishing blocks. These findings advocate further research into the reproductive biology of *N. fucicola* to establish the impacts to egg production from such dramatic variations in growth. The detection of considerable fishing mortality below the legal size limit at certain sites shifts the onus of fisheries management from the live wrasse fishery (which targets fish having benefited from at least 6 years of reproduction prior to the LSL) to consideration of by-catch in the small-mesh fishery. Further research generating selectivities for the gill-mesh sizes used in the small-mesh fisheries would help to discern whether the observed mortality is attributable to such fishing gear.

This study has provided robustly validated age estimates for the commercially exploited temperate wrasse *N. fucicola.* Through the comparison of various growth parameter estimation and growth comparison methods, biologically interpretable comparisons of growth rates have been generated over a broad spatial scale. Correction of age compositions for size-selective biases in the sample gear and consideration of the extent of fishing mortality by site generated robust estimates of age structure over a broad spatial scale and demonstrated the potential for erroneous conclusions if such biases were ignored.

The spatial growth data revealed a positive relationship between water temperature and growth rates and implied that growth in *N. fucicola* was not restricted by density-dependent factors. This has ramifications for the spatial scale of management of the fishery Selectivity-corrected age and size structure revealed an unexpectedly high level of fishing mortality below the legal size limit of the fishery, which also has implications for the management of the fishery. The pattern of low recruitment variability revealed after considerations of selectivity and fishing mortality, supported the hypothesis that *N. fucicola* are well adapted to maximise recruitment in the highly variable coastal hydrography of the east and southeast coasts of Tasmania. In conclusion, this study has increased the knowledge of spatial variability in populations of temperate reef fish and has contributed to an understanding of the post-settlement processes likely to structure them.

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